GENETICS IN SILVICULTURE

Genetics in Silviculture

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PREFACE

FORESTERS the world over will be glad to have from the pen of such a prominent geneticist as Dr. C. Syrach Larsen a work which describes so ably and attractively the progress made in the past quarter of a century in the very important field in which he has been such a notable pioneer.

This book needs no commendation from me. I esteem it an honour to have been the first to have the opportunity to read it in English and sincerely hope that it has not suffered in the process of conversion.

It is a matter for regret that foresters have been so reluctant to accept the importance of genetics in forestry and that so much time has already been lost as a result. The appearance of this work is bound to stimulate an interest in tree-breeding, not only amongst foresters and forest-owners, but amongst all those who are in the least interested in the living tree.

MARK L. ANDERSON.

Edinburgh
February 1956

C. SYRACH LARSEN

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FOREWORD

It is awe-inspiring to see the tallest trees in the world—amongst the Californian sequoias—or to stand in the sample-plot, which Australian foresters have measured amongst *Eucalyptus regnans*, containing the tallest leaf-trees in the world. Both are impressive for their heights, which are a little over 325 feet and a little under respectively. Moreover, the great age of the former, which amounts to from 2000 to 3000 years, is a matter for wonder, while the latter are just as surprisingly young, being only from 200 to 300 years old.

It is just as impressive to make acquaintance with the still untouched forest of Western North America, with its large, beautifully shaped specimens of Douglas fir, red cedar, hemlock, and balsam, majestic because of their age. Unfortunately they are in process of a tragic and all too rapid decline. At the same time it must not be forgotten that the more uniform and much less romantic stands, of only some 80 to 100 years of age, which have arisen after forest fires, can be of still greater value to the timber trade.

In parks and forests in Scotland, England, and other parts of Europe—and, for that matter, wherever trees have been cultivated—it is encouraging to find isolated trees or small groups of trees with unusually fine growth. They strike one as being the splendid remnants of former natural stands, in which their imposing appearance has saved them from the axe, or they have been preserved as rarities, which have originated from the first seed obtained from plant collectors. Although they still remain part of the forest, we must bear in mind that they are past their most favourable economic age, and that greater benefit is obtained from the less attractive, but more uniform forest managed commercially.

Although one's mind is readily attracted by the largest, the oldest, and the finest, which have been given us by nature, one may also have sympathy for the starving people of the world and hope that mankind may be able to secure so much of peace that by co-operation it may be possible to build up rich resources to meet the needs of the individual community and of international trade.

Unfortunately it cannot be forgotten that in his progress and in his use of the riches of the earth man has not been good to the forest. To an overwhelming degree the forest has been an enemy, which has been fought by every means, or else it has been the object of the most intense exploitation by a crude process of " mining " with no concern for the future. Local timber shortages, and to an even greater extent erosion and other misfortunes, not only in respect of the area cleared, but often for agriculture a long way off, have been its direct result on a large scale. Rather paradoxically—but nevertheless with a good deal of truth—it can be claimed that, not until the forest has become rare or approaching its destruction, has an interest been taken in forestry. Those peoples, who first became poor, who first destroyed their forests and were short of wood either had to go under or, having pulled themselves together, succeeded in carrying out the oldest, if laborious, rebuilding of lost wealth by planting and cultivating the forest.

Up to the First World War everything in Auckland was built of kauri, which is one of the world's best building timbers and fetched high prices when exported. To-day one must travel to the most northerly parts of New Zealand to find some small, still untouched, forests of kauri. To see these forests, beautiful with magnificent knot-free stems of that tree, is reward for the journey. Yet in its way it also gives one a thrill to behold hundreds of thousands of acres of Monterey pine in the district around Rotorua. This is perhaps the world's largest and boldest planting scheme with a single species of tree, undertaken over a short period of years. Almost all of it was planted in the depression years of the 1920's, but the work provided food for many people unfortunately placed, and by means of this remarkable tree with an insignificant natural range in California there have been created here by man's efforts very great resources, which are even now already ripe for harvesting.

This is only one of numerous examples, and with the steadily rising appreciation of timber as valuable material for industrial use, and the growing recognition of forests as the necessary protection against erosion and other misfortunes, the planting of forests is about to go ahead with steadily increasing tempo.

It is in this connection that forestry in its silvicultural aspect must turn its attention to the use of genetics. It is by no means my intention to try to establish the overwhelming importance of the inherited characteristics as opposed to those determined by environmental conditions. That becomes very important only as soon as the stage has been reached where seed or plants must pass through our hands, when we are provided with an opportunity of controlling the plant material and providing the desired inherited qualities.

The inherent tendencies are, moreover, of such a nature that, in contrast to important factors of the environment, such as climate and soil, they more easily permit of being altered, and once they have been fixed in the seed they work gratis right on up to the time when the tree is harvested. But we must bear in mind that, in order to build up the tree best adapted to our purpose, we can call upon qualities for doing so only from other living trees. We can obtain the heritable qualities only by selection, by new grouping and other treatment of what we have been given in nature. We must therefore pay just as much attention to the finest products preserved in nature as to the technical possibilities of producing forests. In the task of building up new forests we must not disdainfully or imprudently allow so valuable a tool as genetics to remain unused. Similarly, we must remember that valuable inherent tendencies (genes) may be swept away by irrational felling of remnants of natural forests.

Failure to bring into use so powerful a tool as genetics—one of the strongest forces in nature—will have a restrictive effect upon the development of forestry in line with other land-uses. To work with the means presented to us and in doing so to see new, luxuriant and in their way fine creations growing up may give us a feeling of just as much satisfaction as to indulge in wonder at nature's own wealth and beauty.

As it is not only the silviculturist who contributes to progress, and as most of the application of genetics in forestry is still new, I have tried to present the book in such a way that it is likely to be useful both to those who are to carry out the work and to anyone who feels an obligation to promote forestry.

That Professor Mark L. Anderson, with his knowledge of the Danish language and of the technical nature of the work, has been willing to make the translation, accounts for the presentation of the work in a form which will certainly induce the reader to join with me in thanking him for his effort.

The silviculturist can only endeavour to solve technical details, but the administration in state services and private industries must also be able to assess the opportunities which exist. In the same way the forest geneticist must not be allowed to become isolated. Although he is concentrating upon his task and learning fully to use the science of genetics, he can quite well at the same time be serving silviculture. It is therefore my hope that the book may also find a use as a basis for a series of lectures in the teaching of silviculture.

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Bay of Bengal
February 1955

CHAPTER I

AIM AND POSSIBILITIES

It is not easy to clamber about in tall trees in an attempt to control the pollination of the female flowers brought about by the hand of nature. It is much easier when we bring the flowers down to earth. It is difficult to work, up in the tall larch, which is illustrated in Fig. 1, but after grafting the same tree on to small plants, we can handle the flowers directly, as may be seen in Figs. 2 and 3.

The flowering of the tree is the starting-point of the next generation. The female flowers are fertilized by the pollen, which makes possible the formation of the seed, and endows it with the same effective number of inherent tendencies as have been obtained from the mother. We must therefore, amongst other things, be able to control the fertilization of the flowers before we can hope to carry out an investigation into the inherent tendencies of the trees. Not until then can we attain to new and more valuable types.

The purely practical difficulties of laying hands upon the high-up and not very accessible flowers on our forest trees has certainly been one of the most important reasons why foresters are far behind farmers and gardeners in the use of improved plants.

New and better plants arise by making a selection from those already existing and by combining in new ways their valuable inherent tendencies. If this is to be done in the case of forest trees, it is important to make a beginning before too many outstanding inherent tendencies are finally lost by the unceasing drastic clearances of virgin forests. In addition, the steep rise in the consumption of timber at the present time is a direct inducement to intensive forest management.

In the forestry of the future more and more use must be made of planting; our nurseries must be more and more efficiently managed, while thinning and other cultural operations must call for a constantly increasing investment of capital. Improvement of plant material may also cost much money, but once results have been obtained we have, as it were, something gratis in the future from the fact that they cost very little in maintenance. In this respect improvement differs essentially from many other ways of achieving a greater and better production of timber.

The inherent tendencies (genes), which we have found in nature and, by our skill, have caused to lodge in the seed, will continue to work for us right up to the felling of the tree. An innate capacity to withstand an adverse climate or to overcome disease, a tendency to have more slender branches which fall off more readily and give more knot-free timber, or an innate tendency for vigorous growth can be fixed in the seed and remains as an inherent tendency throughout its whole life. If we are to plant and grow forests, it is thus of the greatest economic importance to seek out and utilize such tendencies. If this had not been done with horticultural and agricul-

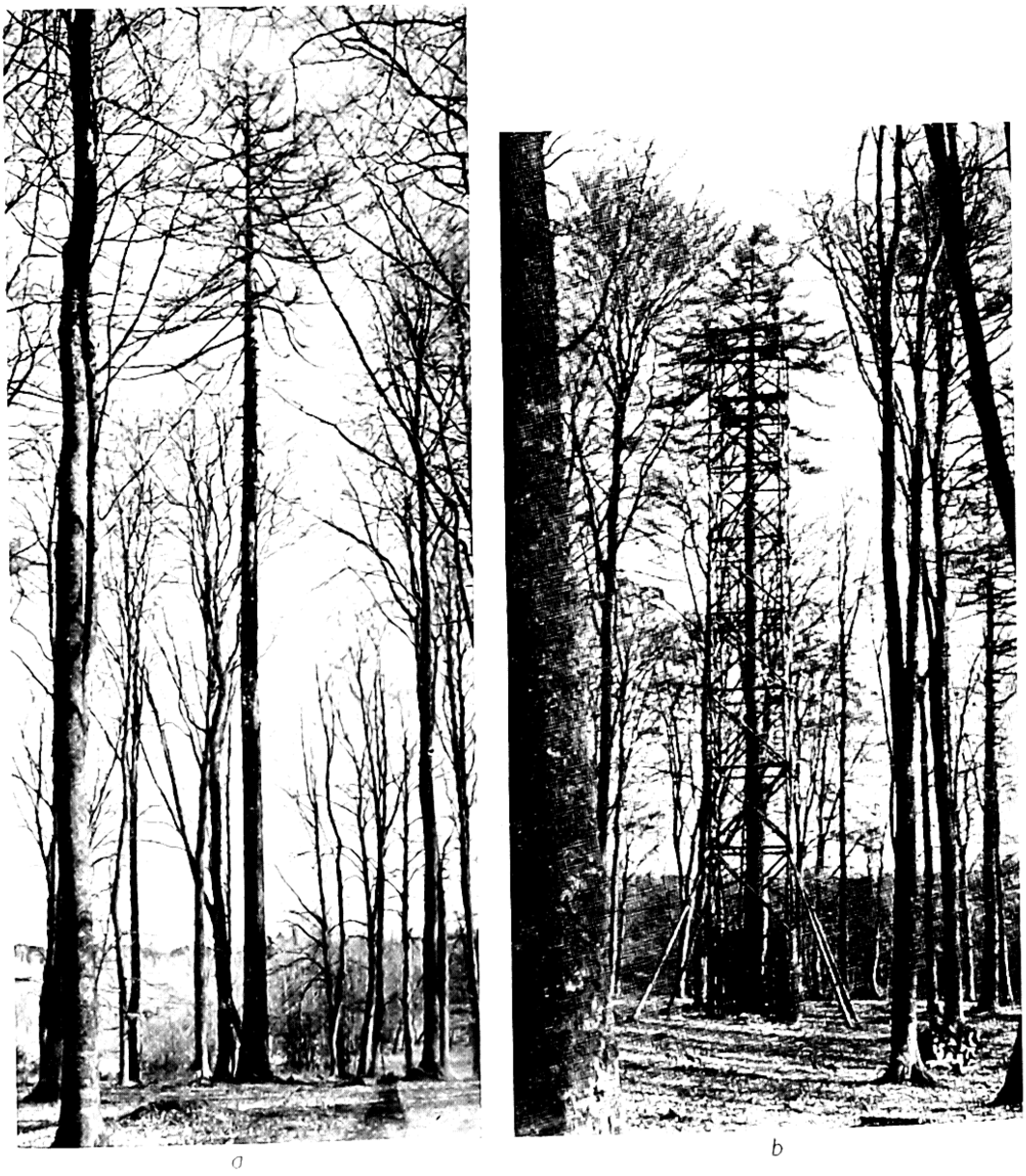


Fig. 1. *Larix decidua*, Mill. Tinghus plantation.
(a) Photograph taken in 1922 at an age of 145 years. (A. Oppermann: Cultivation of Larch in Denmark. *Forstl. Forsøgsv.* Vol. 7, 1923, p. 110.)
(b) Photograph taken in 1935 with scaffolding 95 feet high for breeding experiments. Controlled pollination in the forest.

tural plants, our soil to-day would not be able to support our present large population.

The aim of forest-tree breeding (the task of improving forest planting material) is to establish relationships between forestry, genetics, other branches of plant-breeding, and botany. Of these, the last-named must include, in addition to general botany, special forest botany, plant pathology, and plant physiology. By such co-operation it becomes possible for foresters to make use of already existing scientific results, and to influence future research so that it is directed towards problems whose solution is helpful to plant-breeding for forestry.

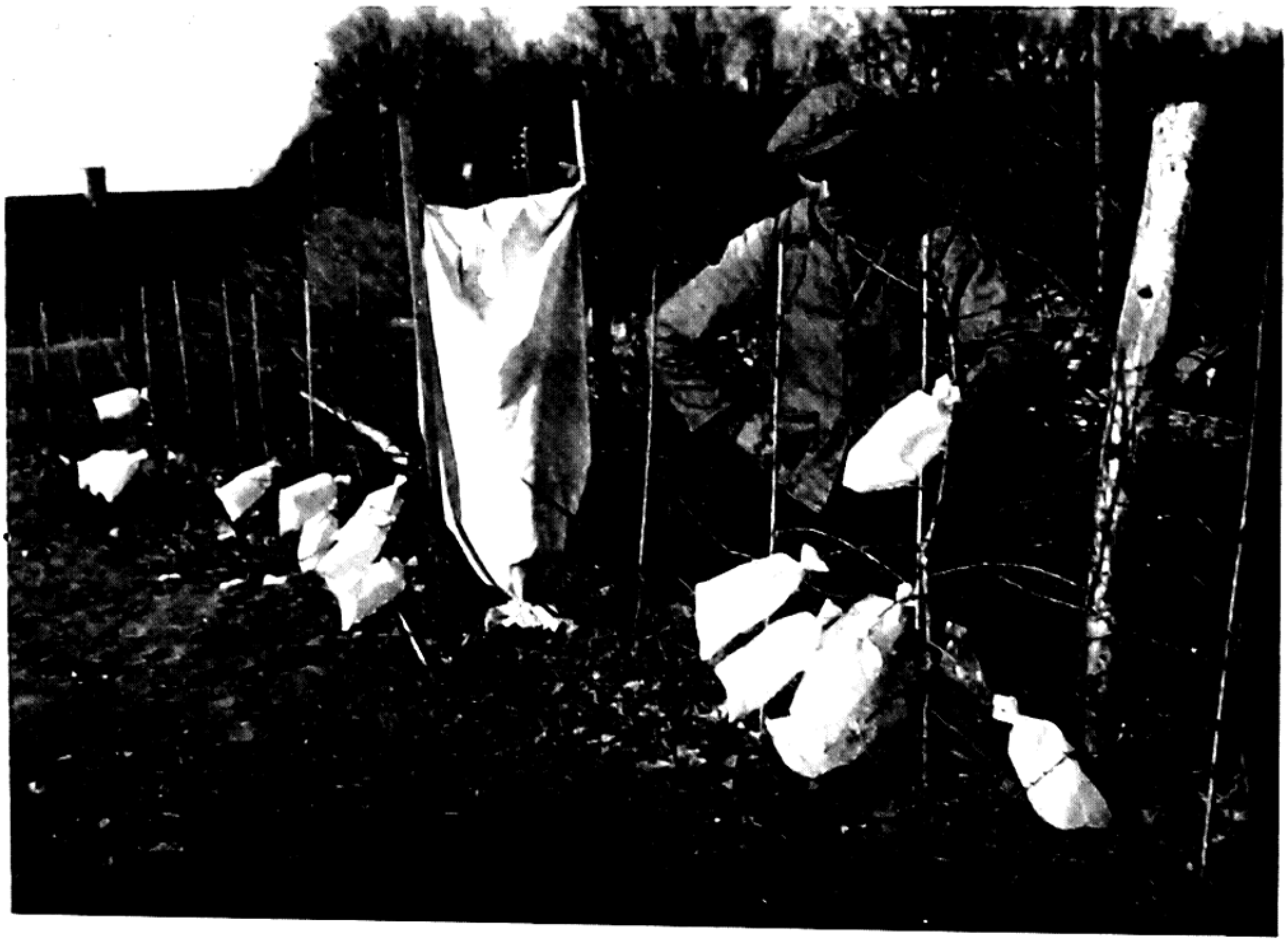


Fig. 2. *Larch.* Controlled pollination of larch in the Arboretum. Grafts from the tree in Fig. 1; grafted in 1936 and 1937. *Photo*, Arboretum, Hørsholm, Denmark, 1st May 1940.

The basis of improvement lies in the fact that not all plants within the same species are identical. Only by using the best individuals can one raise the desired better types, since in part the appearance of the plants is determined by inherent tendencies. Similarly, if it is possible to produce crosses between species, then one can get a combination of qualities from different species.

By controlling the sexual reproduction one can produce " strains " such as we have in the farmer's cereals, roots, and grasses or in many of the gardener's flowers and vegetables which are propagated from seed. These are mostly plants which every year or every other year produce a sexual generation. Because of the rapid succession of generations it has been possible, by constant selection and by artificial inter-crossing, to raise " true-to-seed races ".

In what the geneticists call " clones " we have quite a different kind of strain. These are used in the case of fruit-trees, roses, and other ligneous plants. It is strains—clones—that are widely used in practice in vegetative propagation, which may be accomplished by grafting, budding, cuttings, or layers. From individual plants with desirable pleasant-tasting fruits or unusually handsome flowers, which have arisen more or less accidentally, twigs have been taken for grafting, or buds for inoculating, and these have been transferred on to casual " wildings " (stocks). Each of these strains is thus a single individual, which by division is caused to grow upon numerous extraneous roots when one uses grafting or budding, whereas it has become a number of independent plants, whenever cuttings or layers have been employed.

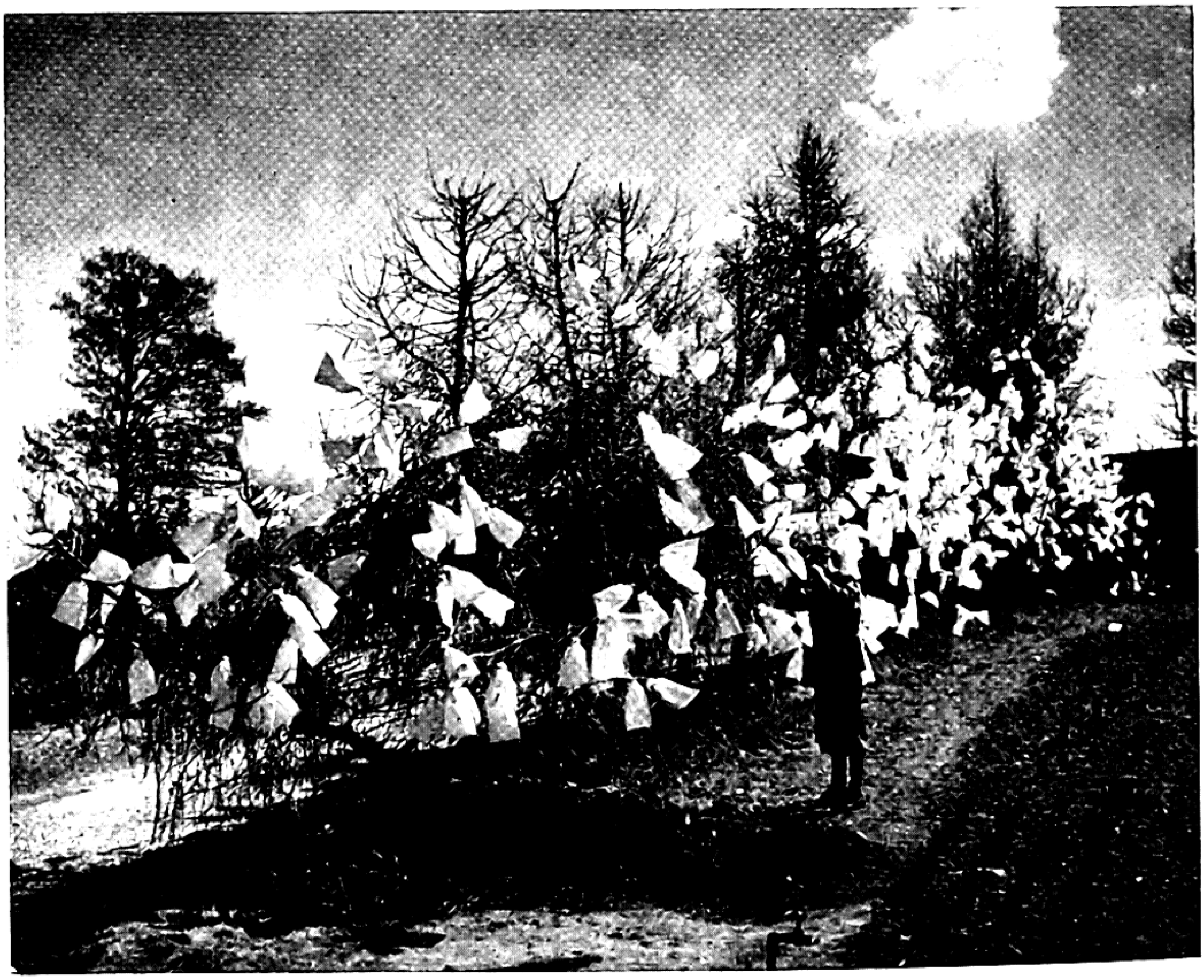


Fig. 3. The same grafts from the tree in Fig. 1. Clone V.44. Controlled pollination with 1650 paper bags isolating about 13,200 female flowers. *Photo*, Arboretum, 24th April 1954.—In January 1955 the seed-yield was 4 kg (9 lbs.) of control-pollinated seeds.

The Douglas fir (V.661) shown in Fig. 66 is an example from a clone of forestry value. It has originated from a single fine tree and has been propagated by grafting.

The method chosen by farmers or gardeners in individual cases of improvement has been determined by the different characteristics of the plants and by the practical possibilities. It has been of special importance to take into account the rapid or slow succession of generations, the time when the male and female flowers appear, whether fertilization is by insects or by the wind, the quantity of seed produced by the plant or its possible sterility and, not least, the capacity of the plant for vegetative reproduction. The last attribute may be so pronounced that it has also been employed in the case of herbaceous plants, e.g. potatoes, tulips, and pelargoniums.

When foresters examined the possibilities of improving their trees, it was very natural that they should first think of the seed, which they were accustomed to use. The idea of raising " true-to-seed races " was not attractive when it was realized that it had to be done on the basis of controlled fertilizations. How could that be done with the flowers high up in the crowns of the trees? The best trees stood, moreover, dispersed over wide distances and they could not be dug up in order to be brought together on a suitable research area. Added to that are the slowly succeeding generations, in which ten, twenty, or perhaps even fifty years have to pass before the new generation can flower and set seed.

There has been the same restricted possibility of making progress with the idea of renewing the forest by vegetative reproduction in the form of graftings or cuttings. The use of cuttings from the cultivation of poplars was well known, but in that case we have the peculiarity that vegetative reproduction is easier than reproduction from seed.

Characteristic of forestry is the community of plants which differ from one another but together form a stand. In a plantation which consists, for example, of one clone of poplar, all the trees make the same demand on light and on other factors because of their identical genetic qualities. The stand therefore becomes differentiated with difficulty into dominant and subordinate trees. Competition is severe, so that heavy thinnings must be undertaken. The material may be of high quality, but the volume of timber per unit of area suffers.

Contemporary with the idea of the easy propagation of poplars, the opinion was reached that one could have such outstanding trees (hybrids), that their widespread cultivation in the form of clones could be justified. This was something quite exceptional. For the other forest trees vegetative propagation was more difficult, and above all there were no prominent isolated individuals with outstandingly good qualities, so that on those grounds alone the possible use of clones was dropped.

Broadly speaking, therefore, even in the most intensively managed forestry, improvement of the stands by the introduction of alien tree-species, and a selection on the basis of free, uncontrolled fertilization, was accepted as proper. However, an important step forward had been made by the recognition of the existence of properties of forest trees dependent upon heredity.

The direct result of this was that people began to procure the best possible seed for new plantations. They began to show reluctance to buy the cheap seed, which was sold with no reliable information about the seed's origin. On the basis of researches into seed of different, accurately known origins, people also got a better knowledge of where the good seed should be sought.

This is the attitude in forestry to-day, even where most progress has been made. In many cases an even narrower outlook is manifest, such that people are glad merely if they can ensure having the desired tree-species planted. Only at research stations are there the first signs of an interest in the improvement of forest trees. The forestry work in this field is of no account in comparison with the marked advance which has been made in agriculture and horticulture. For centuries past they have been ahead of us, and in recent generations they have attained a development with which that in our profession cannot be compared.

The bulky crops of the present day on fields and in gardens exceed by many times the harvests of only a few generations ago. Every country can certainly boast of fine examples of such improvement. As a particularly outstanding example may be mentioned the modern improvement of maize, the so-called " hybrid corn ". The first theoretical research into this was carried out about 1917, and the result is estimated in North America, in the year 1947 alone, to have brought in a surplus income of approximately a thousand million dollars. Such an enormous excess is due to a considerable extent to the fact that the expenses do not differ much as between a light and a heavy crop, whereas the crop-yield is decidedly different. In other words, this is evidence that whenever valuable tendencies have been lodged in the seed by improvement, then these tendencies (genes) work gratis for us.

It is therefore with envy from the forestry viewpoint that we have watched the great progress in other land-uses of the utilization of breeding. It is unfortunate, too, that attention was fixed upon the special difficulties from the forestry aspect and that the matter was dropped. The difficulties are great; they are perhaps almost insurmountable, so long as we follow along the same lines that have been used in agriculture and horticulture. That is just what we should not do; *we should go our own way*, and then the matter appears in a very different light.

If the farmer discovers two plants which, when crossed, furnish fine progeny, then, because of the rapid succession of generations, he can take advantage of this to raise a true-to-seed variety. On the other hand, he has no opportunity of preserving the plants in order to repeat production of the fine progeny observed at the time of the first crossing, for the parent plants quickly die. It is quite otherwise with the forester. When he finds two trees which by mutual fertilization provide the desirable fine progeny, he has scored a success. He can at once proceed to make use of the two trees for future seed-production. By grafting, budding or other form of vegetative propagation he can not only preserve the two trees so discovered for as long as he likes; he can also supply himself with any desired number of new individuals with exactly the same tendency as " the parents ". Every time he discovers new trees, which when crossed with one another furnish a better progeny, he can preserve and utilize them.

The external appearance of a living individual, its bearing, or, as the geneticists call it, its " phenotype ", is determined both by its inherent qualities —its " genotype "—and by the action of external conditions. The good plants are therefore not identical, whether they grow snugly sheltered on good ground, or whether they have to support life on a barren heath. That is also why an oak, which is growing in isolation, has a broader crown than an oak which has grown up in a densely stocked stand. We can go a long way in the " training " of trees under silvicultural treatment, but it is a great advantage not to be forced to use too strict training methods. It is more profitable if we can use trees which in themselves possess inherent tendencies for vigorous growth, straight stems, high resistance to disease against fungi and insects, or which possess other valuable qualities.

Vegetative propagation is of the greatest importance in the improvement of forest trees. Only we have to remember that it should not be employed as the principal means of producing our plants directly. It should not be our aim to base timber production upon the direct distribution of clones in a manner corresponding to that of the gardener, when he plucks his roses or grows his fruits on individuals formed from clones, or as is done in the raising of poplars.

In the improvement of forest trees, vegetative propagation has vital importance as a *technical aid*. By introducing it in our work we have a means to hand for effective creation of a seed-production, which has brought together and combined the valuable inherent tendencies (genes).

Any future task must, however, rest upon the shoulders of the past. Before we begin the task of the future we must, by means of a retrospective survey (Chapter 2), provide ourselves with information about the contribution made by our predecessors. It has not been a small one; it has merely followed other paths, which at the time seemed to be more practicable.

As an example of how things have developed, may I quote some figures from my own country? The area of Denmark is 43,000 km.^{2} (16,600 sq. ml.), of which about one hundred years ago only 4 per cent. was forest. Especially by the reclamation of formerly barren heath, the forest area is now up to something like 10 per cent. In the course of the last fifty years the annual production of timber has doubled, from about 1 to about 2 million cubic metres (27 to 54 million hoppus feet), while the amount of saw-timber has risen in the same time from 90,000 to nearly 1 million cubic metres annually (2½ to 27 million hoppus feet). If all forests are taken into account, so that we include considerable plantations on dunes and heathland, the annual increment is 6·8 $m.^3$ per ha. (75 h. ft. per ac.). The highest production occurs with *Abies grandis* at Bregentved, 1·10 ha. (2¾ ac.), planted in 1926 from seed of Danish origin, which has yielded a current increment of 40 $m.^3$ and now stands with a timber volume (biological) of 444 $m.^3$ per ha. (4885 h. ft. per ac.).

This progress has been achieved by extension of the forest area, by more widespread use of exotic tree-species, careful replanting, frequently repeated thinnings, and better sorting and industrial utilization of the produce. We should make constant use to the uttermost of such possibilities, but we must at the same time push on with breeding. Failure to do so has hitherto been the limiting factor in raising the production up to many times its present size, the possibility of which has been demonstrated in farming and horticulture.

In the last generation, along with the general advance in forestry, a considerable number of progeny researches (Chapter 3) have been initiated, especially by forest research stations.

Armed with our present knowledge we can very easily be critical of particular points in these researches. It is important to offer criticism, when it is to the point. In passing judgement we must, however, always bear in mind that most of the experiments were initiated by members of our profession, who had considerable skill in applying the knowledge of that time. Moreover, we must recognize that time is one of the most difficult factors to control in our profession, so that it is not easy to do things over again.

While we offer criticism we must, therefore, condescend to make use of the material available in the progeny experiments with the utmost desire to get the best possible out of it. We must be very much on our guard against over-valuing ourselves—and on no account be misled into believing that we have now reached the final and correct interpretation of the problems. Along with displaying tolerance in our judgement, we should try to furnish ourselves with the broadest possible basis for the criticism which we may make of the material to-day.

It would not be wise to confine ourselves to a " forestry " review of the results of the research. Before passing judgement let us aim at obtaining an understanding of the natural historical outlook upon the problem as a whole. This applies to the geneticist's clear distinction between phenotype and genotype, to chromosomes, mutations, ecological races, and much more. We should virtually be in the position that we never lose sight of the forestry objective, but that must not lead to a lack of understanding of the knowledge and ideas of others concerning future development.

There is no doubt that the existing older experiments have given us data for a better understanding of whence we should obtain our seed. Of course, the most obvious thing is that they have shown what disasters it may involve not to give precise consideration to the choice of seed for afforestation, especially when it is a case of its having to be brought from long distances. A more exact examination of experiments and a more widely organized international co-operation in connection therewith nevertheless gives much useful guidance.

It is an urgent matter to plan as well as to initiate new progeny researches, and it is necessary that there should be many of them. It has to be remembered, however, that by each of these researches, work and responsibilities are stored up for the future. Occasionally one may find that their popularity is in eclipse. It is advisable to keep in mind that time is precious. Therefore we must dip into the events of the past in order to utilize the material in the most effective manner. Since foresters, botanists, and gardeners have been particularly active through the ages in moving about and raising tree-species to an extent far beyond the experiments laid down by the forest research stations, it will be of value to turn our attention to what they have done. It may be possible to find other valuable progeny experiments—perhaps even " cultivated types " formed under man's influence (pp. 22 and 41).

Where, from the point of view of time, it is not so important whether one uses a greater or lesser number of generations in order to reach some desired objective, it may be debated if it is more advantageous to work with a large amount of material in free, uncontrolled pollination rather than choose a more limited number of plants for controlled fertilization. Even with annual plants, it may be essential to control the fertilization, so that one has an exact knowledge of both the mother and the father. While working towards a desired objective in the progeny, means are provided for an analysis of the inherent tendencies contained within the parent plants.

Controlled pollination (Chapter 4) is carried out by protecting with a bag or some other means the female flowers against pollen conveyed to them naturally. Instead, it is collected from the desired male plants and transferred by our intervention on to the female flowers. (Figs. 7 and 8, Chapter 4, pp. 45 and 46.)

This sounds intricate, and it is even more complicated when it is a question of forest trees. In this connection, however, two alternatives must be considered. The one is to wait for an interminable number of years for a somewhat unreliable result, while the other is to work more energetically for a shorter period of years. It has been shown by research that by controlled pollination, rapid and valuable progress can be made in forest-tree breeding.

By controlled pollination there is complete assurance that the qualities found in the progeny can have been transmitted only through the two known parent plants. The valuable qualities of a progeny will not only be available for use in future breeding, but simultaneously with its appearance parents will have been ear-marked, that can be retained and used again in a constantly repeated production of the progeny which has once been proved to be a good one.

However difficult controlled pollination may seem, it is the simplest way of reaching within a limited period of years definite information about the value of individually selected trees for breeding. That is the line to take, and in following it we are fortunate in having the help of vegetative reproduction (Chapter 5).

In forest-tree improvement we should not attempt to choose between vegetative reproduction in clones and the sexual procedure in arriving at true-to-seed strains. We should combine the two methods. By their combined application the means are provided of considerably shortening time and reducing the importance of distance.

Grafting and other forms of vegetative propagation have been known in gardening from the earliest times and there is nothing new in grafting forest trees, but the essential thing is to appreciate its importance as a technical aid in their improvement. It is laborious to clamber about in the trees in order to control the pollination of the flowers, and it is quite out of the question to dig up the selected trees and bring them together on our test area. What we want is not the whole tree, but only a vegetative part, which contains exactly the same inherent tendencies as the tree. Twigs, buds, pieces of root, or any vegetative parts of the tree whatever, which are used in reproduction, contain all and only the inherent tendencies (genes) specific for the tree. Such a vegetative part differs essentially, therefore, from a seedling, of which the tree has been the mother or father—or perhaps even both these parents—for such seedlings contain only a selection of the tendencies contained in the tree.

For example, by grafting or taking cuttings from a selected tree we can thereby produce for ourselves plants with exactly the same inherent tendencies as occur in the high-lying flowering branches, or any other part of the tree, from which twigs are taken. Vegetative propagation can, moreover, be carried out in different ways, and the material be subjected to very varying treatment according to the purpose of the plants. It may contribute to the saving of much time to investigate the inherent tendencies of the tree, and at the same time its breeding value, by both the sexual and the vegetative methods. This would almost eliminate the significance of distance, as the living, vegetative material, in the form of scions, for example, can without difficulty be shot down from tall trees, sent over long distances and, after appropriate insertion, brought into early flowering or used to test directly the qualities of the vegetative material.

In the large crowns of the selected trees there will be such a quantity of twigs that we can at once proceed with a multiplication of genetically identical plants in very large numbers. Thus we can preserve the selected trees as living specimens in any desired number and in the manner most appropriate for the continuance of the work. This is an insurance against retrogression, which is otherwise to be feared from the felling of the finest trees in the forest, and it gives us easy access for undertaking controlled pollination and furnishes us rapidly with abundant material for any analysis of the inherent tendencies of the trees.

This chapter commenced with a reference to Figs. 1, 2, and 3. We must consider these illustrations more closely. The first shows probably the finest larch (*Larix decidua*) in Denmark. Around the tree may be seen the scaffolding from the first attempt to carry out a directly controlled pollination. It was costly and difficult. It seemed far easier to do the four-year-old graftings shown in Fig. 2.

The graftings from the original tree were made in 1936 and 1937, and sixty-eight individuals from them were planted in a row 35 metres long, shown in Fig. 2 and Fig. 3. When the sixty-eight plants were five and six years old respectively they bore in all 3805 cones. Fig. 3 shows them at seventeen and eighteen years of age in the spring of 1954, when together they were able to accommodate about 1650 bags for the isolation of about 13,200 " female flowers " (cones).

By obtaining easy access for controlled pollination of such a large number of female flowers of completely uniform material from a genetical point of view, which is at the same time one of the tallest trees in the forest, the breeder of forest trees puts solid ground under his feet.

If desired, all the female flowers can be used for fertilization by a single similarly selected male. In this way one can obtain a really numerous progeny, in which all the plants are related in the first degree, and in which the mother and father are selected good trees. On the other hand such a fertile mother, which in good seed-years may furnish fifteen thousand to twenty thousand seedlings, can also be assigned to several fathers. If, for example, pollen is used from ten other larches, one might be successful in obtaining ten progenies each of one thousand five hundred to two thousand plants. These could be grown under identical conditions, and in that way we would come to have ten sets of plants of identical age, the differences between which would be determined by the different fathers alone. This kind of analysis is valuable and it must therefore be recommended that the work of improvement should be taken up as soon as possible in order to provide large clones from individual outstanding trees.

Controlled pollination by means of bags and artificially transported pollen is solely a task for our research work. The position is quite otherwise when the intention is to make use of the results obtained. As soon as one knows —or merely has good reason to suppose—what parents will be valuable in breeding, one can go on to seed-production in seed-gardens established for the purpose (Chapter 6).

By far the largest number of forest trees are wind pollinated, and this has been a serious obstacle to the idea of bringing pollination under control in such a way that the seed can be produced in sufficient amounts and cheaply enough. Although pollen may be borne long distances with the help of the wind, there are nevertheless limits to the distance it can reach in quantities of practical significance. It puts one in mind of alcohol, which it is expensive to produce when absolute, but cheap to turn out in its 96 per cent. form. For our researches we must have complete certainty, but in the production of seed for practical use it is without significance if there happens to be some small effect due to strange pollen.

For practical purposes it is not difficult to locate areas which are fairly well protected from the pollen of a single tree-species. It is there that we should establish our seed-garden and plant out clones, from the individual trees which we have found, or selected seedlings obtained from controlled pollination of such trees. In that way it will be possible to harvest, in large quantities, seed which has arisen only by reciprocal pollination between genetically valuable plants. By vegetative propagation we can speedily produce large quantities of genetically identical plants (grafts, clones) from selected trees, studied in detail. It thereby becomes possible within a limited period of years to produce seed by controlled pollination in any desired amount.

This will have special significance for the production of seed for hybrids, and thus for making use of heterosis in plant improvement in forestry.

As mentioned, controlled pollination is the simplest way to secure knowledge about the value of trees for breeding. An important step in this direction, however, is to be able to identify the good genotypes, and for that the employment of " tree-shows " (Chapter 7) has proved to be useful. These are groups of plants reproduced vegetatively, in which each group represents one tree (a clone) and which are located in such a way that they can be subjected to comparisons. This can be done by placing several clones under the same conditions, or the individual clone can be tested under different conditions.

This is our means of obtaining in the course of *a few years* some idea of those qualities which have caused a tree to have the capacity in the course of *a long period of years* to develop into an extra-good tree, so instead of waiting for many years it can help us to make a rapid analysis of the past. Although it does not provide the complete answer to the problem of good breeding material—i.e. plants for our seed-gardens—it nevertheless goes a long way towards doing so. It offers the opportunity for a great deal of analysis of what has once been accumulated, so from that, fresh building material can be selected, which has already demonstrated its good qualities.

It is not advisable to draw up rules about how these good qualities should be assessed. These will depend upon local requirements, which in turn will often vary with the tree-species. Attempts to embody them within some form of scheme or fixed framework can be misleading. Broadly put, it may be said that they should comprise requirements in respect of growth, form, and health. Of these the first is easy to measure, and therefore at once attractive as a basis of comparison. It is also very important, but not altogether easy, to distinguish it from the last. The collective result depends upon both, and in the same way diseases may also have considerable influence upon both the form and the growth of the tree.

As it is our object to see that plants are produced with as many good qualities as possible, we must try to assess them separately. For that we have tree-shows, where clones can readily be distinguished by their growth and form. Although we ought to show optimism, we must not be too credulous. It should be remembered that reliability is a very important factor. On account of the long-term rotations in forestry, the problem of disease is one of special importance. It is therefore made the subject of more detailed mention later (Chapter 8).

It is important in this field of work to maintain close co-operation with plant pathology and forest zoology. It is possible for us through our tree-shows to present the "patients" in such a way as to be extremely inviting to specialists for further studies. We must seek to expand co-operation for the benefit of our silviculture, and that can best be done by making direct use of these sciences in forest-tree breeding. From amongst those individuals which by thorough tests can show themselves to be resistant to disease, we should select our breeding material.

Without the help of plant pathology it has happened in practice that resistance to a disastrous disease has come into use as an important factor when intercrossing in a tree-species which has fine qualities but is liable to disease. This happened in the case of the hybrid larch first used in Scotland (Chapter 9). After its introduction into Scottish silviculture the European larch showed itself to be liable to larch disease (*Dasyscypha Willkommii*); under cultivation, however, accidental crossings occurred with the coarser but disease-resistant Japanese larch. The result was excellent disease-resistant plants of decidedly vigorous growth.

This is an example from which it is useful to take a lesson. The tendency towards resistance against disease due to heredity comes in this case from an alien species. Research into several tree-species, however, has shown considerable individual variation in their behaviour towards diseases. In the case of trees, in the same manner as practised on a large scale for herbaceous plants, it will often be possible to get control over such an attribute merely by searching within that species.

Furthermore, the hybrid larch displayed a well-marked vigour of growth as a result of the cross between two species. Instead of allowing this to occur as the result of crossing between casual individuals, it is more fitting to make use of it as a " culminating effect " between previously selected outstanding trees of the two species. It is an easy transition from this to the production of seed in large quantities by vegetative reproduction and convenient association in seed-gardens.

The peculiarity that two individuals " alien " to one another should, by reciprocal crossing, produce progeny of specially vigorous development is known as hybrid-vigour; in genetics as heterosis. With the hybrid larch this arose through individuals from two species established by taxonomy. There are other examples of valuable species crossings in forest-tree improvement; but it is by no means necessary that the individuals should belong to different species. They can also be trees of one species, but of different geographical origin, different ecological strain or type, which have become different from one another after deliberate inbreeding. By using the last-mentioned procedure in agricultural plant-breeding in recent years the example of " hybrid corn " given above has been obtained.

Such striking results of hybrid-vigour have been demonstrated that the Danish geneticist, MOGENS WESTERGAARD, in a statement quoted again later (Chapter 10, p. 171), has said: " It can scarcely be doubted that the heterosis method is the answer to breeding difficulties due to cross-fertilization. In fact it eliminates entirely the two unsolved problems, determination and fixation of the good genotype."

We should be grateful for such encouragement, just as we should actively seek to work on a genetically unimpeachable basis. That is the absolute pre-requisite; the slow succession of generations in forestry calls for this in a special degree (Chapter 10). This does not preclude independent initiative in any way. Although in our methods we adapt the work in accordance with forestry conditions, we can likewise have the benefit of following the latest progress in agricultural plant-breeding.

Reference has been made to hybrid corn. In this connection attention should also be drawn to " combining ability ". In heterosis it is the combination of the two parties " alien " to one another that is decisive. In respect of combining ability it is a quality hereditary to the individual itself which produces the effect. We speak of high and low combining ability. If it is high, then the plant has the attribute that when crossed with others it increases the productivity of the progeny, whereas plants with low combining ability, on the other hand, drag the progeny as a whole downwards.

It is therefore just as important to be on the look-out for the low, as to get hold of the high, combining ability. It is the latter which can imprint the valuable hereditary character on the " family ". For finding such plants, workers in Denmark, the U.S.A., and Holland have, independently of one another, devised the so-called polycross method. (See amongst others H. N. FRANDSEN (1940) in *Imp. Agr. Bur. Joint Publication No.* 3, H. M. TYSDAL, T. A. KIESSELBACK and H. L. WESTAVER (1942) in Coll. Agr. Univ. Nebraska, *Agr. Exp. Stat. Res. Bull.* 124; S. J. WELLENSIEK (1947) in *Mededelingen Landbouwhogeschool* 48.)

The polycross method is prized in agricultural plant improvement for its applicability in the case of cross-fertilizing plants, which can be divided into clones and preserved as such for a number of years, and it is just as suitable for our forest trees. Thus there is a contact between genetics, agriculture's latest plant-breeding work, and our still young improvement work with forest trees.

Thanks to the advanced state of affairs in genetics and plant-breeding in other land-uses we can directly pluck many of the fruits of their work. Incorporation of these with methods necessary for forest trees may lead to an assurance of extraordinarily rapid application of results.

CHAPTER II

RETROSPECT

NOT so long ago, in the author's youth, his distinguished teacher the Danish forest geneticist A. OPPERMANN recalled to memory the work carried out by DUHAMEL DU MONCEAU. It is no longer a new idea in these days to stress the importance of inherited qualities in trees. It is more remarkable that the statements published in the literature of the past two hundred years should not before this have made a stronger impression. It is often a long way from the written word to the adoption of something in practice; in the field of forest genetics this development seems to have taken place particularly slowly.

In *Des Semis et Plantations des Arbres* (pp. 85–87) DUHAMEL as early as 1760 published fundamental observations on hereditary behaviour in forest trees. Of the oak (*Quercus robur*) he says that small acorns may furnish good trees, while from a large acorn we can obtain a small tree. Nor does the form offer us any reliable indication, since seed from a stunted tree produces ugly trees, if it is stunted by nature, but can produce fine trees, when the difference in its form is due to injuries.

From our forestry history we know that prominent Danish foresters were in touch with DUHAMEL. OPPERMANN therefore put forward the view that DUHAMEL's opinions may have had an influence upon the choice of seed round about the time when a vigorous movement for encouraging forestry in Denmark had just made its appearance. Regarding a prominent forester of that period, it is known that when ordering seed of Scots pine (*Pinus sylvestris*) he required not only that the cones should be gathered from a distinctly named locality, but that they should also be collected from the largest " mast-trees ". It was the same forester who, in 1777, procured the seed for the larch stand, in which the magnificent tree, often mentioned later (Fig. 1), is still preserved.

DUHAMEL's words have not remained unheeded, and it is possible that they have contributed to furthering interest in the problem. In this connection it should be remembered that there was a close contact at that time between gardening and forestry. Two hundred years ago the cultivation of trees in gardens and parks had long been known; many of the first plantations in forests are reminiscent of the painstaking plantings of gardeners with attention paid to the individual plant. Several of the men who published the first books in support of silviculture were also well known in horticulture.

Before the book mentioned above, DUHAMEL also published works on gardening, and he was in reality a plant physiologist. EVELYN, BURGSDORF, and other writers of that time also reveal much understanding of the growing of trees in gardens and parks. The oldest Danish text-book on silviculture (1779) is a comprehensive work of more than seven hundred pages, and it was followed three years later by a similar book on horticulture. They were by the same author, who also published works on natural history and agricultural economics.

We may be critical to-day of these old works and think that forestry then stood at a very primitive level, and in a sense that is true; but we must not overlook the fact that the old literature gives expression to many valuable contacts with professions from which forestry at that time had not yet completely divorced itself. Moreover, old plantations are still in existence, as for example, the splendid beech-trees in the Forêt de Soignes (Belgium), and something so exceptional as one from graftings of pines in the forest at Fontainebleau, which are clear reminders of a close link with gardening.

We foresters are all proud of the progress of our profession during recent centuries, in which, from a slender beginning in conjunction with other land-uses, with botany and very often with sport, it has grown up to be an independent profession. Silviculture now rests upon a solid natural historical basis, and we have advanced far towards the economic constitution of forests, which are wholly and solely the result of the work of foresters.

At the same time it may well be deplored that in our drive for independence we have omitted to carry grafting knives and failed for a long time to occupy ourselves with the inherited qualities which are so important. While we have been dealing with other more urgent problems, both agriculture and horticulture have celebrated triumphs through making use of the inherited qualities in their plant material.

We have to go back to about the years 1820–1840 in order to meet with any movement in support of a better understanding of the behaviour of inherited characters in treees. At that time PHILLIPE-ANDRÉ DE VILMORIN laid down experiments, which later clearly showed that species of forest trees could be broken up into climatic races. This was a " botanical " piece of work, in respect of which unfortunately forestry again displayed its independence by leaving it unheeded.

C. FISCHBACH was himself a forester, and his articles appeared in the *Allg. Forst- u. Jagdzeitung* (1848) and the *Zentralblatt für das gesamte Forstwesen* (1900), so that they should have had a better chance of holding the interest of forestry. It is significant that there are fifty-two years between his first and his last papers. Already in the first of these, in 1848, he recommends that extensive forestry work should be undertaken in this field, but at the same time expresses his dubiety about being able to get foresters to take an interest in "solch minutiöses Detail der Forstwirtschaft". He obtained a sorry recognition, in spite of the fact that he believed he had made the interesting discovery that the beech (*Fagus sylvatica*) could be self-fertilized. He also claimed that he had demonstrated by experiment that the fastigiate growth of the fine oak at Harreshaussen (*Quercus robur* var. *fastigiata*) was hereditary. This led him to recommend experimental planting with the use of seed from a small number of selected, specially valuable trees, and he also stressed that they must be chosen in isolation from one another and from other trees of the same species.

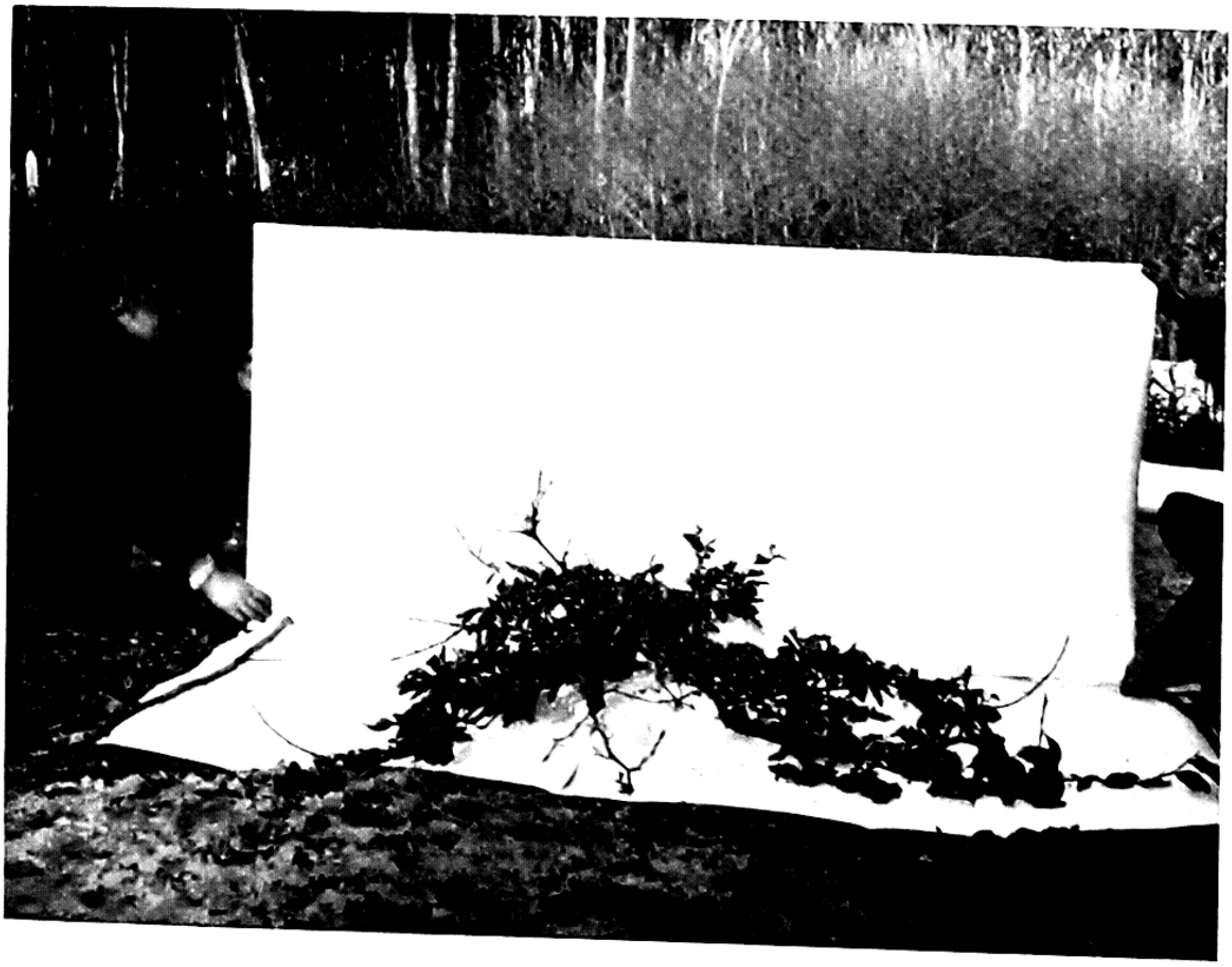
Somewhat later M. KIENITZ (1879) deplored the one-sided interest of foresters in the introduction to Germany of new, alien species. He considered it of more urgency to strive after an improvement of those species already present and better known.

Although there does not seem to have been any fruit from the efforts of these men to induce foresters through the professional literature to undertake the work, reference may be made to a single example from practice (*Zeitschrift für Forst- und Jagdwesen*, 1888). This is mentioned in more detail under "Breeding of Larch" (p. 175) and we shall merely remark here that the KRÖMMELBEIN referred to succeeded in making selections covering six generations in one type of larch, and we should add that he was trained as a gardener. The work obtained local recognition, but has not been further appreciated or utilized.

In a curious way the use of exotic tree-species rather harshly condemned by KIENITZ had an effect in fixing to a greater extent the attention of foresters upon the inherent tendencies contained in the trees. With the more widespread use of exotic tree-species the seed-trade experienced a considerable improvement, and at the same time, because of easier means of transport, use was made to a greater extent of commercial plant nurseries. This appeared to be economically sound because it provided forestry with greater quantities of suitable plants. It meant in addition, however, that foresters to an appreciable extent lost their direct contact with the place in which their plants had been produced. The seed was harvested in far-distant countries, and it often happened that the same species was imported from very different regions, so that very varied results were obtained. This began to have its effect in the period prior to 1900, and with the revival of the theory of heredity about the turn of the century it became urgent to subject the problem to further trial from a genetical point of view.

Fig. 4. *Beech*. The "Fasanbøgen", a freak form, with A. Oppermann beside the original tree. (*Forstl. Forsøgsv.* Vol. 2, 1908, p. 67).

Fig. 5. *Beech*. Seven-year-old plant from seed from the tree in Fig. 4. (*Forstl. Forsøgsv.* Vol. 2, 1908, p. 40).



Before 1900 CIESLAR in Austria and ENGLER in Switzerland had carried out experiments which clearly demonstrated the existence of climatically determined races of Norway spruce (*Picea Abies*). Both further extended their experiments to include other important species, and similar experiments were carried out in other places. It was found through these that variations depending upon the source of the seed were so striking that the problem of the geographical origin of the seed attracted great attention. Examples quickly came to light, in which for a single species there were greater differences in the production of the forest due to the source of the seed, than in the production due to growing different species. A valuable tree, indigenous to the site, may also prove to be without forestry value in the form of offspring from seed obtained from a foreign country.

This meant that provenance trials became very popular. The experiments were constantly extended, and from striving to demonstrate the best possible results they gradually changed over to attempting to find through them types of special value. This was, in fact, one project which directly strengthened international co-operation amongst forest research stations.

Pioneering works on the recognition of inherent differences in the form of trees of the same geographical type were brought out by CIESLAR and OPPERMANN at the beginning of this century. Both were particularly interested in the so-called freak (" *vrange* ") forms and used seed from single trees or small groups of markedly poor form for comparison with progeny from trees valuable to forestry. The inheritance of fastigiate growth in oak discovered by FISCHBACH was, in addition, confirmed. The work was taken up in Sweden by HESSELMAN and SCHOTTE, and in the U.S.A. by MUNGER at the North-west Forest Experiment Station near Portland. There they went on to work with progeny from individual trees from a single locality.

The importance, demonstrated in so many quarters, of both securing seed from the proper geographical region and getting it from appropriate trees was valuable encouragement to display greater concern about the choice of seed. A proposal put forward by the Swedish forester and botanist, V. T. ÖRTENBLAD, in the last year prior to 1900 for a more active improvement work on the basis of selection of single individuals was, on the other hand, not followed up.

Based on the reflection that the important German forest trees are wind pollinated, F. v. LOCHOW (*Der Züchter*, 1929) concludes that the attributes of the mother must be predominant amongst the progeny from the individual tree. In an investigation into Scots pine (*Pinus sylvestris*) he therefore collected seed from a series of specially good mother-trees for several years in succession. He further tried to arrange the progeny he raised in such a way that they could easily be compared and preserved, so far as possible, in order to furnish seed for further use. This is a fulfilment of similar ideas of which

ÖRTENBLAD had previously made himself the spokesman, and the geneticist, ERWIN BAUR, had explained the method in *Grundlagen der Pflanzenzüchtung* (1921).

It is worth remarking that v. LOCHOW, by the procedure mentioned, had already found appreciable differences in the progeny between trees that were identical in appearance (phenotypic). In one case (tree 49) he described the progeny as " on average considerably higher, with healthy vigorous stems and a plentiful supply of dark green needles ", whereas another progeny, " number 50 on the other hand has already suffered severely from blight, so that a large number of plants have failed, and those remaining are noticeably poorer than the neighbouring lot". He had thus already brought to light resistance to disease as an inherent character, and had in fact shown it to be true for a serious disease of an important forest tree.

v. LOCHOW also found that the colour of the seed was characteristic of the individual tree, in which he was in part supported by HESSELINK in Holland (*Mededelingen v.h. Rijksboschbouwproefstation*, 1922). During the years 1910–1922 the latter had observed the seed from sixty different trees of Scots pine; although on the main point he reached the same result as v. LOCHOW, nevertheless he found that the circumstances were more complicated. In this connection reference may be made to some observations based on extensive material by the Danish botanist, C. RAUNKIAER, on the shape of acorns (*Dansk Bot. Tidsskr.*, 1933). They may be summed up as a means of distinguishing in the case of oak a series of forms, which can be described as iso-reagents.

Following upon the results of the many experiments which had been carried out in the first twenty to thirty years of this century, complete certainty had been reached as to there being a considerable genetical variation in forest trees. It was generally accepted that the source of the seed from a geographical viewpoint was of decisive importance, while there was also apprehension about getting seed from poor stands. The first step had also been taken towards a deliberate improvement, although the aims still did not go beyond selection on the basis of free uncontrolled fertilization.

This implied that increasingly greater efforts were made to obtain the best possible seed for the regeneration of the forest. A demand arose for more and more detailed information about the origin of seed and plants; people were no longer satisfied with information in more general terms. The demand arose not only for information about the precise location of the place of collection, but a knowledge was also sought regarding the quality of the stand, from which the seed was collected.

As a direct result of this, systems of control of seed and plants came into operation in several countries. The control of plants has most interest for the individual country, whereas the control of seeds is of considerable international value. F.A.O. and the International Union of Forest Research Organizations have in recent years done a great deal of work in this field. The task has above all been directed towards ensuring that each of the participating countries should of itself try to promote legislation and voluntary agreements for control of the local seed-production and seed-trade. Besides serving to the direct advantage of the country, this will mean an important step forward as regards mutual co-operation. There still remains much to be accomplished, but this merits attention.

In addition to making use of climatically determined types and the best of the naturally occurring stands, the opportunity also exists of discovering types which may originate under the influence of man. As examples of this, attention can be drawn to the Dutch avenues of oak and to European larch and Douglas fir in Scotland.

During the last sixty years acorns from Dutch avenues have been regularly introduced for use in Danish forestry, although we have plenty of acorns here in this country. Already the selection, which has been done in choosing plants for the avenues, seems to have affected the progeny to so great an extent that, even under our conditions, it furnishes material of high quality. Apart from the fact that, amongst other things, Danish forestry can take advantage of the selection undertaken earlier, there is great encouragement to be derived from this. It is a pointer towards the possibility of securing a considerable improvement merely by a very simple choice and use of free fertilization. The progeny seems to have been markedly affected by the fact that the smaller plants were not included in the avenues, and the pronounced ascending branches indeed seem to indicate that there has been a rapidly accomplished improvement into an " avenue-type ". Although there may be some doubt about the benefit of having acute branch-angles, it nevertheless offers a strong incentive for similar building up of locally valuable plants.

The types of European larch and Douglas fir in Scotland, with peculiar features, were obtained in rather a different way. They have both been derived from a few specimens, from which, by constant home breeding and growth under silvicultural attention, there seems to have been produced an isolated type of uniform character. As interest becomes keener in such possibilities, there should certainly be other examples like this in both the old and the new worlds.

Although it lies rather outside the scope of forestry proper, reference should be made to the widespread cultivation of *Hevea brasiliensis*. By far the greatest part of the world's consumption of raw rubber is derived from trees which have been planted far from the natural range of the tree-species. The cultivation was initiated on the basis of a relatively small number of plants. This was again a case of isolation under the influence of man, and it is well known that much progress in improvement has been made.

Isolation can, especially when it is the subject of painstaking application (Krömmelbein's larch), imply definite advantages. Since time is costly, and we must therefore make use of all the available material carefully, we ought to study it thoroughly. It may become of value for continued improvement, although there may also be some risk of having had too limited material at the start. Valuable attributes may thereby have been left out, while the selection may not always have been made from a forestry viewpoint.

The work towards improvement through the use of hybrids and artificial pollination has been more deliberate, and has been undertaken either for direct utilization in forestry or as a means for obtaining information on the significance of inherent characters.

Numerous hybrids have been described botanically from their occurrence in the boundary zones between the systematically established species. They have arisen even more abundantly where the species which occur sparingly have also been collected into parks and botanic gardens. This has been of special importance for diœcious trees like poplar, which have shown a marked tendency for mutual crossing and at the same time possess a well-marked capacity for vegetative reproduction by means of cuttings. This has led to the widespread use of the hybrids in clones.

Because of the often strikingly vigorous growth and in other respects remarkable qualities of the accidentally produced hybrids, they soon attracted attention. When they arose in tree-species which did not readily permit of reproduction by cuttings, and for which the only solution seemed to be to preserve them through graftings or buddings, it was only the task of the gardener to utilize them. Better-known examples are *Platanus acerifolia* (*P. occidentalis* × *orientalis*), *Tilia vulgaris* (*T. cordata* × *platyphyllos*), and *Ulmus hollandica* (*U. glabra* × *foliacea*). These are dealt with in more detail under hybrids, where it is also stated that Klotzsch, as early as 1854, tried to direct the attention of foresters to the forestry value of hybrids. However, this remained just as unheeded by forestry as the American walnut hybrids produced by Luther Burbank in 1877–1878.

It was the hybrid larch in Scotland that first attracted genuine interest from foresters, and ever since the first detailed description of it in 1915 it has been the object of much attention. Here they were seeing something really new, which had not simply arisen from the abundance of forms in nature. It was realized that here had been obtained a combination of valuable attributes from two well-defined species, and that by their crossing they had furnished a progeny of hitherto unknown vigour of growth.

It came to be widely propagated from the source of its first discovery, and other opportunities have fortunately also been found for its production, where Japanese and European larches happen to have been planted together.

Rapid steps were also taken to test the progeny of the hybrid larch, which has often been called F_2, although it might with just as much reason be presumed to have arisen by reverse crossing back to one or other of the parent species. Amongst it, good material was again found. There was a desire to make use of this, but there was little certainty in its production of seed, as this was based solely on free pollination in stands, which had not been established, moreover, with that special object in view. The production of seed was accepted as a kind of by-product, the opportunity for which occasionally seemed to occur. Not even in this case, where is should have been an urgent task, was there any change-over to making a distinction between seed-production and the usual forestry object of producing timber. This was conducive, in spite of everything, to a limited use of the hybrid larch, and it contributed to much uncertainty.

In order to study the inheritance of the various types of branching in Norway spruce, N. SYLVÉN in 1909 initiated experiments in self-pollination, the progeny from which was used for comparison with plants resulting from free fertilization of the flowers. This was a very valuable move, which SYLVÉN regrettably did not have the opportunity to follow up directly. Artificial pollination was used thereafter in an early experiment at Placerville (California) for producing the hybrid *Pinus radiata* × *attenuata* (1928), and A. DENGLER likewise, on the basis of controlled pollination, carried out valuable experiments with *Pinus sylvestris*, of which he gave a report in 1932.

A special opportunity to have interest drawn towards these problems was presented by A. J. KOLESSNIKOFF's reading of his contribution *"Über die Notwendigkeit, die Probleme der forstlichen Genetik und Veredelung . . ."* at the International Congress of Forest Experiment Organizations in Stockholm in 1929. He then gave a review of experiments in self-pollination in several species of common oaks, limes, elms, birches, and pines. He had obtained satisfactory results from these with the exception of experiments with Scots pine, from which he obtained no progeny; but he himself added that the factor responsible for success may conceivably be present in other material of the same species. KOLESSNIKOFF stressed, with much force, that it was of the greatest importance for improvement in the future to have these problems elucidated. Thus it may prove possible not only to have valuable self-pollinations carried out, but perhaps also to take inbreeding a stage further from there.

There have thus arisen over a period of years not a few very strong arguments in favour of controlled pollination in forestry experimental work. Perhaps even more noteworthy is the fact that proposals have been put forward for taking up vegetative reproduction.

The Swedish naturalist GUNNAR ANDERSSON had already come forward in 1906 with a plea on these lines. With great enthusiasm he advocated that foresters should choose good seed-trees in the finest stands, and that it would be a great advantage to follow the example of gardeners and use grafting on a wide scale. This does not seem to have been pursued, and the same applies to a detailed programme put forward in 1922 by the German, L. FABRICIUS, for an improvement in forest trees. FABRICIUS is in agreement that forest trees can be reproduced vegetatively, and can thus be multiplied for the establishment of plantations with the sole object of producing seed. About the same time the head of the Danish Forest Research Station, A. OPPERMANN (1923), mentioned in a work on the larch the possibility of grafting the most valuable trees so as thereby to make it possible to obtain more seed. It is astonishing that none of these pleas made any impression in forestry experimental work. The authors allowed the matter to be held up by these theoretical considerations, and the " sound-barrier " could not be broken by any means. Our profession had isolated itself too effectively, and it would have to take some other line in order to make headway.

Along quite different lines and without the use of artificial pollination and vegetative propagation of LANTELMÉ sought to obtain better seed by artificially inducing the setting of seed on selected trees. In the *Zeitschrift für Forst- und Jagdwesen* of 1933 he announced that success had been achieved by strangulation in getting a beech some thirty years of age to set seed for six years in succession. He also mentioned other results, which would indicate the possibility by artificial interference of getting even older trees to bear fruit without the " seed-years " occurring at intervals of some years. LANTELMÉ's work was carried out in Germany where, owing to the course of events, it has been impossible for him to make headway. The question of the possibility of its practical realization therefore still remains an open one. Particularly for a tree-species like beech, with its markedly long intervals between seed-years, it would mean a great advantage, if a desired number of selected trees could be brought into regular annual flowering. In otherwise " barren " years one would thus be able to ensure getting seed by mutual pollination only between the selected trees.

The Americans were the first who had the temerity to give a forest research station the title of " tree-breeding ". This was the Eddy Tree Breeding Station at Placerville (California), instituted in 1925. It was established by private initiative, but was later linked to the Forest Service under the name of the Institute of Forest Genetics. Ever since its foundation the genus *Pinus* has been in the forefront as the object of the work of the station. In the eastern U.S.A. about the same time a task, similarly restricted to the improvement of poplar, was taken up. With the support of the Oxford Paper Co., A. B. STOUT and E. J. SCHREINER carried out a good many crossing experiments, by which they succeeded in raising valuable new types. This attracted attention and gave reason for entertaining greater hopes of further improvement of forest trees. The work was later linked to the Northeastern Forest Experiment Station.

Poplar was also the first object of attention of a forestry section organized in Germany at the Müncheberg improvement station. Under the guidance of W. v. WETTSTEIN at the beginning of the 'thirties, controlled crossings were initiated in greenhouses. WETTSTEIN showed that branches cut from poplar can be made to flower and after controlled pollination to give ripe seed. This was a great advance, as it thereby became possible, to an entirely different extent from previously, to organize on sound lines the work which WETTSTEIN himself advanced a long way. From this institute, moreover, there later came valuable contributions in the shape of descriptions of pine progeny.

Because of its easy production of hybrids, and the direct applicability for use of the results obtained by the employment of vegetative propagation, poplar was specially inviting as a subject of improvement. In addition to the places already mentioned, it has been used by PICCAROLO in Italy, HEIMBURGER in Canada, and many more. It has also been much handled by research stations set up by industry. Of these may be mentioned the Institut de Populiculture at Grammont in Belgium, the Swedish match factories' research at Mükinge, and the Hellestrup Nursery instituted by the Danish match-makers. The last-named was established in 1942 and has worked principally with aspen, whose cultivation it has caused in a remarkable way to be incorporated into practical forestry. International co-operation is considerable, and is looked after by the " International Poplar Commission " in conjunction with F.A.O.

In 1935 H. NILSSON-EHLE found in Sweden the triploid aspen (*Populus tremula* f. *gigas*) as a modified large-leaved form in the forest. It was of particularly vigorous growth and furnished a very promising material for improvement. Through private initiative the " Föreningen för Växtförädling av Skogsträd " was founded in the following year. NILSSON-EHLE was the driving force in the early years. N. SYLVÉN became the society's first director, and the later internationally famous Ekebo and several auxiliary stations were established.

Although the genus *Populus* in this case, too, happened to yield material for the first sensational results, the institution expanded very quickly and strongly by absorbing a great deal of improvement work under its wing. Because of NILSSON-EHLE's discovery of triploid aspen and his tetraploid plants rapidly raised from it, cytological work came to occupy a predominant place. With great energy early contact was also sought with practical forestry by the registration and utilization of *élite* single trees and stands in the case of a number of important forest trees.

On his own initiative BERTIL LINDQUIST about the same time carried out active work in Sweden in favour, particularly, of utilizing the narrow-crowned Scots pine. By the combined action of a body of men in Swedish forest industry a society for " practical forest-tree breeding " was formed. Under its auspices LINDQUIST carried out important work, which contributed to a steadily increasing interest in the utilization of the best material in breeding, and HOLGER JENSEN (Ramlösa Nursery) revealed similar independent initiative. In 1946 the State Forest Research Station in Sweden set up its own section for forest genetics under the leadership of Professor ÅKE GUSTAFSSON.

In the other Scandinavian countries of Norway and Finland, and in Great Britain, Holland, Belgium, France, West Germany, Russia, Austria, Yugoslavia, Switzerland, U.S.A., Canada, Australia, New Zealand, Japan, Korea, and possibly even more places, forest genetics sections have been instituted in conjunction with other forestry research work, or facilities have been allowed for individual persons to concentrate on the work. I have ventured to name only the countries mentioned above, because of personal relations with them, but even more might perhaps still have been named. There are thus plenty of opportunities for international co-operation and for local carrying-out of the work.

In Denmark the first controlled pollination was carried out in 1924. Since 1930 controlled pollination has been used on a large scale, and in particular a series of rather successful pollinations in the early years with larch, encouraged the continuation of the work. In the spring of 1934 I had the first graftings of ash with material from selected breeding-trees. After that, vegetative propagation in conjunction with controlled pollination became the basis of the development of forest-tree breeding in this country. Broadly speaking, it has followed the lines which I mentioned in the same year in a paper on forest-tree breeding, from which the following is an extract: " I strongly urge, therefore, taking up vegetative propagation and, in conjunction with experiments in artificial pollination, the establishment of seed plantations for the supply of seeds for practical use." (*Royal Veterinary and Agricultural College, Copenhagen*, 1934 *Yearbook*.)

At first the work was undertaken in the Forest Botanical Garden, which was founded in 1838, and which, with its old seed-bearing trees of numerous species, offered a favourable opportunity for the controlled raising of hybrids. In 1936 a new arboretum was established, which, along with the old establishment, formed a section under the Royal Veterinary and Agricultural College. Forest-tree breeding has therefore been able to derive benefits from a close association with other sections of the college, namely, forestry, horticulture, botany, and genetics, while at the same time finding it possible to maintain an independent initiative in the devising and applying of methods of improvement.

At the same time it has been possible to develop close co-operation with the Danish Forest Experiment Station, and that, amongst other things, has been very important in obtaining for use material from the older sample-plots, while it has also been possible to establish valuable direct contact with both state and private forests. Moreover, it is fortunate that the administration of forest-tree breeding at the Arboretum has been kept to a relatively modest plan and, instead of expanding, has time and again contributed to the setting-up of new institutions.

It has been particularly useful that the State Forest Service should have established its own Plant Breeding Station in 1947. This has as its aim to undertake practical improvement work in the state forests by selection, vegetative propagation and the establishment of seed-gardens. Although the first of these are now beginning to give seed, it is of great importance that, when the station was erected, there was built right away considerable storage space with controlled temperature and humidity for storing seeds over quite a long period of years.

The first step towards any improvement in a country's supply of forest seed must be to avoid the use of the poorest seed. With the irregular seed-setting of the majority of our forest trees, there is a considerable danger in poor seed-years of having to use seed of less-good quality. It may be somewhat rash to do so, but one may almost say that in the poor seed-year there is a great opportunity for the seed-trade to offer seed from far-distant regions, which have had more abundant seed of a species in demand. As we now know, it is far from satisfactory to get seed merely of some desired species. The seed should also be from stands suited to the climate and satisfactory from a forestry point of view.

Before the station was set up, research had been initiated which showed the possibility of preserving tree seed in a viable state under control even over a considerable number of years. It was fortunate for our forestry that the State had shown how to apply this knowledge in practice. It has turned out to be the first important step towards a better supply of seed, and it is equally handy, moreover, for use in storing the desired seed coming from the seed-gardens, thus ensuring its being put some day to the most economical use.

Private forestry is also beginning to make use of results of forest-tree breeding. It has formed an association with its own consultant, and it is establishing its own seed-gardens and tree-shows, and there is great enthusiasm to make use of the best possible seed in the association's forests.

The intensive forestry in our country, in which nearly all regeneration—

even without the co-operation of plant-breeding—is based on artificial sowing and planting, has been responsible for the development of the last twenty-five years. Forestry was already adjusted to take advantage of every advance in the provision of better plant material. A similar rapid development may be expected in Great Britain, where forestry will to a great extent have to be built up on afforestation, and it will, moreover, be remarkable for the overwhelming use of exotics.

The English have the very expressive term "green-fingered", which applies to a person with a special aptitude for propagating plants—and while they have the term, they also have plenty of folk to whom it applies. If we can induce such worthy partners to take part in forest-tree breeding by vegetative propagation, it will be extremely encouraging for the work.

This applies not only in Great Britain, but wherever intensive improvement of forest trees should be taken up. We must turn back to the time when forestry freed itself from its link with horticulture and forgot to take the grafting knife with it. The oldest living reminder of that time is a remnant of the graftings of Corsican pine on Scots pine in the Forest of Fontainebleau, already mentioned, by J. C. LOUDON (*Arboretum et Fruticetum Brit.*, 4, 1838, p. 2130). There were in the years round about 1826 "several thousand trees every year" raised in this manner, while the grafting knife was diligently used throughout Europe in the early years after the introduction of new tree-species of value in the forest; but unfortunately this could be done only in gardens and parks, in which they had the sense to preserve the rare or specially beautiful trees.

Just as we must learn to apply gardening methods in using the vegetative process of breeding our selected trees, so also must we to a great extent intensify co-operation with botany, genetics, and other subjects. Just as we were long ago induced to build up our profession on a sound natural scientific basis, so now must we also take up vegetative propagation, which gardeners have used with so much success, and we must not overlook the significance of controlled pollination. We should employ isolation bags, artificial injection of pollen, even greenhouses, refrigerators, and many other technical appliances, which have been brought into use in other forms of plant-breeding.

It is exceedingly important that every move on the way forward should be adjusted to suit forestry conditions. Foresters must not therefore delegate this task. We can attract fellow-workers into our profession, but the forest economic goal must not be lost from sight. Although it is a serious objective we keep before our eyes, and although we should be foresters heart and soul, it may also be regarded as an attractive form of sport.

To hunt after the finest stands and those individual trees of the forest which furnish the highest yields, both in virgin forests and in the more civilized, well-managed forests, is in many ways reminiscent of the hunter's search for the finest heads. Instead of slaying the quarry, is there not more sport in producing from it fresh living material with desirable qualities? In this " retrospect " we have been able to inquire into a prolonged and in its way limited development; but we are now at a stage from which important future objectives can be viewed.

CHAPTER III

PROGENY TRIALS

It is not at all easy to assess from the external appearance of a tree what will be the value of its progeny. It becomes even more difficult when the progeny grows up under different external conditions, as, for example, when it is transferred to another region of the globe. A tree may be so stunted by storms or frost damage, or it may be so starved by poor soil, that it may be difficult to recognize it, when one is accustomed to see the species elsewhere as a valuable forest tree of large dimensions. The Douglas firs highest up on slopes of the Rocky Mountains bear no resemblance to the magnificent trees of the lowlands and sheltered valleys. In Norway, as well as in the rest of Scandinavia, the Scots pine is known as one of the predominant forest trees of the highest economic importance, for it occurs in extensive stands of fine, straight stems. It looks quite different when it forms the last remnants of forest towards the top of the mountains or on the outermost coastal stretches of Norway exposed to the stormy Atlantic ocean. Out there it has to creep and twist so that it may become just as low and scrubby as the Mountain pine in the Alps of Central Europe.

In spite of their very varied growth and form, however, the botanists are not in the slightest doubt as to what is a Scots pine and what is a Mountain pine. It is, in fact, possible to establish that it is one and the same species of pine, *Pinus sylvestris*, which we find spread over most of Europe and a large part of the north of Asia. Its range extends over 30 degrees of latitude and no less than 123 degrees of longitude. Between its most westerly and most easterly occurrences there is a distance equal to over a third of the circumference of the globe. In the same way the botanists bring together all the Douglas firs from the Californian coast to the interior of Colorado, and with a range from south to north of more than 27 degrees of latitude, into the single species of *Pseudotsuga taxifolia*.

On the basis of external, morphological features, the systematic botanist goes even further and divides up Douglas fir, for example, into three geographical varieties—the coastal and lowland varieties, *viridis*, the northern type in the Rocky Mountains, var. *caesia*, and the variety *glauca*. Similarly for the Scots pine, some few geographical forms have been distinguished and described on the basis of morphological features.

Such a subdivision is, however, far from sufficient for the forester, who to a great extent distinguishes a varying quality in trees and stands, often over very short distances. These distinctions can be determined genetically, but before we concern ourselves with that, an attempt should be made very briefly to give a review of what is the modern outlook on the concept of species and of the development which has taken place in our understanding of it.

As early as the eighteenth century, LINNAEUS and his followers carried out crossing experiments which indicated to some extent the possibility of the appearance of plants outside those species and varieties generally regarded at that time as being rather fixed and immutable. About one hundred years ago the Frenchman, ALEXIS JORDAN, showed by experiment that within certain species there were differences in the progeny of populations from different growth-sites. From this he deduced that such species consisted of a larger number of populations different each from the other, which he designated new minor species. Light was thrown on the position in respect of forest trees by PH. A. DE VILMORIN, who laid down experiments in the period 1820–1840, from which it was later successfully proved that *races of forest trees* existed, and it was to the greatest detriment of forestry that these discoveries were not directly utilized in afforestation.

Through the works of CHARLES DARWIN, who showed the importance of natural selection in the formation of species, a clear understanding was reached of the frequency of *variation* in nature. As early as 1865 GREGOR MENDEL had discovered the fundamental principle for our comprehension of the inherent factors, in that by his researches he had demonstrated the existence of *inheritance-bearing* units. This had no effect, however, until MENDEL's laws were rediscovered in 1900. They were followed very speedily by WILHELM JOHANNSEN's distinction between *genotype* and *phenotype*. Thus it was exactly at the beginning of the present century that there was a great advance in our understanding and utilization of the science of heredity.

The phenotype of an individual is its external appearance, and that is the product of its genotype and of external influences. This is also expressed by stating that the phenotype is the reaction of the genotype under the given external conditions. From that it next became possible to work with the individual inherent tendencies, which are called genes, and a very rapid development ensued.

The recognition of *chromosomes* as the inheritance-bearing elements, in which the genes were located, led to very rapid development of cytogenetics in particular, while progress was also made in understanding mutations. *Mutations* are sudden, fitful changes in the genetical constellation and they may consist of loss and gain or break-up of genes (inherent tendencies). They occur in nature, and can be induced during experiment by various external influences such as toxic substances, temperature and radiation. They are of the highest significance to our understanding of the formation of species and types, as they form, as it were, new elements in evolution.

In the early nineteen-twenties GÖTE TURESSON's works appeared, which showed that species with a wide range are composed of series of "*ecological races*" differing from each other, which make it possible for the species to invade places with ecologically different conditions (*Hereditas*, 1922 and 1925).

Our understanding of evolution is thus now based on a knowledge of the free combination of the inherent tendencies (genes) combined with gene-mutation. We likewise know that, besides leading to the formation of species and varieties, they are the basis for the existence in species of mutually different *ecotypes*.

In addition to the subdivision of a species into morphologically different geographical varieties, it can be broken up into physiologically different ecotypes or local populations, which are all determined by heredity. By experiments with certain herbaceous plants, which it has been possible to break up into clones, these important points have been beautifully illustrated by J. CLAUSEN, D. KECK, and W. M. HIESEY. (*Experimental Studies on the Nature of Species*, Carnegie publ. No. 520, 1940, and No. 564, 1945.)

For us foresters it is easy enough to find a desirable species and even a geographical variety characterized on the basis of external features, but it is quite another matter to define physiologically different ecotypes or to prove the value of the seed from a local population. Concerning these physiological qualities—so important for the forester—only experiments can provide us with reliable knowledge.

As the forester, however, from practical experience early became aware that it was not a matter of indifference whence he obtained his seed, even when it was of the right species, research work in forestry has been undertaken to reach an understanding, and make use, of variation in species, especially with reference to climate.

This work consists of forestry *provenance trials*. A considerable number of these exist in respect of several important tree-species, undertaken partly locally and partly through international co-operation. The assessments already made show with complete clarity that several tree-species display great differences when seed is used from a series of geographically distinct regions.

So long as we are working locally and our sole problem is to fence the natural regeneration or supplement it by planting trees indigenous to the site, the matter is of no interest. Similarly, neither do we turn our attention to the question when it hinges upon small variations, because a forest stand—in contrast to many other forms of produce—is peculiar, in that only a small number of the plants which grow up reach appreciable size or maturity. For that reason alone there has to be an appreciable difference in the seed-lots used, in order to be able to perceive (in the long run) any distinctive, genetically determined, qualities.

The problem aroused greater attention when it became usual to transfer seed for forestry purposes over long distances. With progress in forestry and more painstaking replanting there arose a trade in forest-tree seed and plants. Both the forest-seed trade and commercial forest-plant nurseries have been of great assistance to forestry, but it is nevertheless true that in many countries, especially in Europe, poor results were obtained owing to a very indiscriminate moving around of plant material.

For England and Scotland poor central European Scots pine was obtained instead of trying to make wider use of the indigenous far more valuable types. For districts in Europe with a continental stamp of climate Douglas fir of pronounced coastal forms was, on the other hand, secured. In Denmark we obtained some of both, besides oak of southern French origin and other objectionable imports of tree seeds.

On the basis of provenance trials which had been made and of studies in nature it became clear that, in transferring a tree-species for use in forestry, one had to make certain, in the first place, that one was making a transfer between climatic regions as similar as possible. *The general rule* which we follow to-day is therefore that so far as possible we must work with seed from one and the same climate. This offers the greatest assurance of avoiding unpleasant surprises.

We must not remain satisfied with that, however tempting and obvious it may sound, because it is only one part of the problem. The problem of the forester is not merely to reclothe a devastated area with a stand just like the one that has been cleared away. It is his task to seek for opportunities to put it into a better state, more valuable for forestry. In addition to being on the look-out for types moulded in nature in accordance with ecological conditions, we must be very much alive to variations in respect of qualities of value in forestry.

It should be our task to study nature and imitate it in such a way that we do not employ violence in making absurd transfers of the tree-species. The capacity of the species to develop ecotypes and local populations not only shows us the great difference which exists between extremes, but gives us an insight into the great possibilities in natural variation. Within a " hardy type, of less vigorous growth ", there is a regular variation in growth-energy, just as a " frost-tender, more vigorously growing type " varies in hardiness. We have only a slight knowledge as to what extent that is so, and therefore difficulty in perceiving the procedure we should adopt in order to obtain the most strongly growing and at the same time hardiest types.

Just as, from the provenance trials so far carried out, we can confidently say that care has to be exercised in making transfers, so, too, there are experiments which show extremely varied results from using seed from a series of individuals which must be deemed to belong to the same ecotype. This has been shown in respect of branch-types in spruce and of growth-energy and form in oak, beech, spruce, pine, etc. Trials are still far from being so intensive, however, that they can fully explain the facts. They have at best merely shown us examples of existing differences. We do not know whether these represent extreme points, or how the variation is distributed in different directions. It is therefore necessary that we should continue these trials.

On that point everyone can surely be in agreement. We are in a state of uncertainty; but there are possibilities of making progress. Even now we have to use large quantities of seed for forest plantations and we must thus try to use the best possible on the basis of our present knowledge. The forestry problem is very different, however, in different parts of the world.

Where it is merely a case of getting a new vegetation to grow similar to the recently cleared or formerly prevailing forest, we work with greatest assurance when we take seed from the same region or a region with a climate most like that of the same region. Where land is expensive and forestry is carried on intensively and is based on planting or artificial sowing, and where the objective is, by the best possible planting and careful thinnings, to achieve the highest possible yield, there will be a tendency to try out other methods. In such circumstances it is natural that we should try to use seed from regions where the desired species has developed especially well, or at any rate has developed better than in the previous stand, without the climate being at the same time too divergent. While fetching the seed from the better stand, it will usually be desirable to be able to take it from the " same climate ", but preference must be given to making greater demands upon the quality of the stand than the most severe requirements in respect of climatic resemblance. Add to this that the climate is only a part of the ecological environment—and how can we really find over wide distances identical ecological conditions? The ecological environment represents such an interplay between the chemical and physical state of the soil and the climatic factors of rainfall, temperature, wind, light, and much more, that it is in a way reminiscent of the richness in natural variation of the tree-species—and indeed of the individual ecotype.

In our search for opportunities of transferring the tree-species it is extremely important to confine ourselves to the problem of the minimum factor. There is a good deal to show that we must pay attention to it in just the same way as is done in assessing the nature of the soil. It is possible that it may be an advantage to restrict ourselves to a greater extent to the decisive factors, rather than to look for agreement in all particulars. *Taxodium distichum* in its native habitat in south-east North America is restricted to swamps and river-banks, so that abundance of water seems to us a necessary factor of its ecological environment. Here in Denmark with a very different climate it does very badly owing to the coldness of the water; it reaches the best growth here on drier and at the same time more sheltered localities. At the limits of its possible cultivation it may be better able to do without plenty of water rather than warmth. In the same way it is astonishing to see *Quercus palustris* as a prominent avenue tree in the drier conditions of Canberra, whereas in its native habitat in eastern North America it is remarkable for occupying the flat land along the rivers, where there are frequent floods.

When transferring our tree-species from one region to another it is important to remember that, as opposed to agriculture, we are excused from demanding homogeneity in the seed used. For us foresters it is not so important that a seed-lot should furnish a uniformly better progeny; it is far more important that it should contain a certain small proportion of seed with attributes of specially distinctive, higher quality. That is therefore a question which it is important to take up in planning progeny trials. It is not only a case of establishing a sequence of intermediate qualities, but also extremely desirable to obtain information about the degree of variation of the qualities within the individual lot of plants.

The Danish forest seed merchant, JOHS. RAFN, after many years' experience, became an advocate of " climatic deceptions ". By that he meant that a greater advantage was obtained by being to some extent optimistic, and by taking the seed from a region which might indeed be said to have a rather more favourable climate, but on the other hand contained more valuable stands, than merely by going to the region on the whole most similar in respect of climate. Such a view was confirmed by experience with Norway spruce in the most southerly part of Sweden and in Denmark, which are both without natural occurrences of spruce. In the introduction of that tree-species into cultivation a substantially higher yield has been obtained by using seed from more southerly regions in central Europe than by using seed from the natural, slightly more northerly occurrences, from which it must be presumed to be travelling south.

Regarding the Norway spruce the position in Scandinavia seems to be such that it migrated northwards to the east of the Baltic Sea and passed through Finland down the Scandinavian peninsula. It is quite likely that on its travels it has lost genes (tendencies) for vigorous growth, while it has at the same time become a more hardy type than we now find in central Europe. The use of generations of Norway spruce from central Europe shows that it is sufficiently hardy with us and in south Sweden. We are thus also in a position to make use of the greater growth-energy of this type. At the same time, experiments with seed from stands which are better from the forestry aspect within the natural range of the species are to be urged, although we should simultaneously search farther afield from our own country and nearer to the place where the tree-species has its " optimum ".

On exposed localities one might be tempted to use seed of spruce from a definitely northern locality, in order to secure in that way a very hardy progeny, although one might expect a rather weak growth-energy (increment). This has indeed been tried, but the result was quite otherwise. Spruces from seed from Rovaniemi in Finland (67° North Lat.) were induced in the milder climate of Denmark (56° North Lat.) to come into leaf so early that year after year they were damaged by night-frosts and looked very miserable. The best results so far in this country have been procured with spruces from seed from Romania (46° North Lat.) and it does not come from a region with a " similar climate ". It comes, on the contrary, from a locality where the decisive factor (some element of climate) has given it the quality (late leaf-flushing) which so acts that with us it can also display its favourable growth. It has a vigorous growth but at the same time it has so late a leaf-flush, that it escapes the destructive late night-frosts and can thus steadily increase its lead.

It is not enough to talk of conveying seed from regions with a " similar climate ". What does that really amount to? We have to split up the concept of climate into its individual factors—and be rather bold. The aim must be to import the best qualities from regions whose limiting factors allow it. Moreover, in speaking of climate we are too prone to confine ourselves to items that can be measured, such as temperature and rainfall. Other ingredients of " climate " may be equally important and so in the long run our observations should not merely be restricted to climate, but should refer to all the ecological factors.

In this connection reference may be made to the work carried out by F. W. WENT at Pasadena, California (F. W. WENT, 1950: "The Earhart Plant Research Laboratory," *Chronica Botanica*, Vol. 12, pp. 93–107). He reached important conclusions by isolating the individual climatic (ecological) factors, under laboratory conditions. (Compare also W. M. HIESEY: " Growth and Development of Species and Hybrids of Poa under Controlled Temperatures," *American Journal of Botany*, 1953, Vol. 40, pp. 205–221.)

Should it happen to be possible in connection with forestry to invest capital in such a costly research apparatus as was used at Pasadena, it would be gladly welcomed. I have no doubt that experiments with clones of forest trees in that way will be able to furnish very rapid and valuable guidance in the forestry of the future. When we really set out to re-orientate the timber production of the world from being a simple utilization of the virgin forests to a well-planned cultivation—away from " mining " and towards " land-use " —then the talk will be of such high capital values that research on these lines will prove to be very profitable. It will be possible to attack the problem at its source, and to place forestry in a position to utilize a wealth of results discovered by plant physiological science.

The majority of workers in genetics are to-day quite unanimous in their view that there is a danger of the science of genetics becoming isolated because of its hitherto lightning development. There is a need in respect of all forms of plant husbandry for increased co-operation between geneticists and plant physiologists, from whom the former originally broke away, and the same applies to the plant pathologist, who has likewise shown a tendency to go his own way. We must hold together and keep our sense of perspective; the work forms a biological entity. This is nowhere more important than in forestry, which has not yet moved very far from the untouched types of the primeval forest—or from " weeds ", if you like.

It is very common in European forests to use tree-species from the virgin forests on the west coast of North America. If in this work it is desired to use in cultivation in western Europe seed from the natural American stands, one must begin with a climatic comparison of the two regions. From this it will quickly be seen that it may be quite difficult to discover regions which agree from the ecological point of view. It is extremely difficult from the fact that we know all too little about the interplay of the factors or their effect individually, and about how they actually set limits to the use of the type. In the next place we do not know much about the background of the present natural distribution of the tree-species. Is it a tree-species in retrogression or is it advancing to cover a greater range, and by what route has it arrived at the areas it now occupies? We must ask ourselves whether the Sitka spruce has its present peculiar distribution in the narrow belt along the Pacific coast because it cannot do without the proximity of the sea, or is it because it there reaches its predominant position in relation to other tree-species, which are to a greater degree held in check by the proximity of the sea? If the latter is the case, then we can with reason attempt to use it in pure plantations on areas much farther from the coast than where it is now growing.

Besides the problem of the ecological adjustment of a tree-species for a certain region, we must take into account the mutual struggle between the tree-species, in which the more light-demanding must give way before the more rapid-growing and more shade-bearing species. The tree-species, also, are far from uniformly endowed with a capacity to resist or to return after forest fires or other catastrophes. Abundance of seed which flies easily or a capacity for producing suckers may also be of importance in this connection. Tree-species like aspen, both *Populus tremula* and *P. tremuloides*, are markedly favoured in this respect.

The struggle between the tree-species has to a great extent been the determining factor in their present distribution. As an example may be mentioned the Monterey pine (*Pinus radiata*), with its remarkably small natural occurrences on the Californian coast. This tree has been taken from there for use in afforestation in Australia, New Zealand, Latin America, South and East Africa and other places, where in pure stands, with no competitors for the light, it has attained a development which far exceeds that of the natural stands. This seems to show very clearly that this tree-species owes its present very limited natural distribution to the effects of an unequal struggle with other tree-species which have simply been unable to follow it on to the last narrow coastal strips. Around it a natural barrier has been erected against its expansion, and its occurrence by the sea shows it can put up with the proximity of the sea but does not tell us if this is a necessity for its success. Without man's intervention we should know nothing about this matter, and what it could otherwise do. We should be very careful not to overlook the significance of such " small " species, because they may conceal much of value which they have simply not had an opportunity to show.

Nor can we assume that nature is obliged to take forest economics into account in the mutual struggle between the trees. The tree-species which take the lead in the mutual struggle to take over new territory must do so on the basis of their inherent tendency for natural variation, and thus are able to establish themselves as an ecologically defined type adapted to the site.

If we think of a tree-species advancing northwards or up a mountain slope, in order to gain a foothold under more unfavourable conditions, the more robust and more heavily fruiting individuals must have better opportunities to do so than, from the forestry aspect, the more valuable and slender individuals, which may not produce so many offspring. Under other conditions innate characteristics, such as straight and rapid growth, which are more in harmony with our forestry requirements, may have been the decisive factor in the type produced on the site. We can presume this to be the case, but we do not have much opportunity under natural conditions of forming any reasonable opinion concerning the factors which have made their influence felt during the movement of the tree-species to its present position.

The majority of our economically important forest trees are, moreover, peculiar by being long-lived, and by reaching to a great height and by scattering their pollen from there in immense quantities. There is a complex of factors which must be assumed to contribute to the mingling of tendencies to bring about natural variation. Strictly speaking, we have to admit, in any event, that we do not know what this kind of pollination means. That does not by any means imply that we should ignore the significance of the ecologically evolved types; but it has been stated in order to stress that the problem must not be considered too narrowly in our search for the best possible and most suitable forest types.

We must try to combine the experience gained from our studies of ecologically determined types with investigations into the variation of attributes of forestry value in the case of single individuals from a presumed common ecotype. Our knowledge in this field is still so limited, and the possibilities so great, that simple rules cannot be given regarding the procedure to be adopted in our choice of seed. It is dependent upon so many factors and local conditions, that in individual cases great circumspection must be shown. It is right to be careful and to try only to use seed within, so far as possible, uniform regions; but if agriculturists had confined themselves merely to doing that in their efforts to increase our crop-yields, things would not have gone so well. Foresters would be wise to display a reasonable optimism by simultaneously making use of seed from the best possible stands. How far we can go in this it is possible to find out only by experiment, but painstaking studies of individual cases can provide us with a basis for orderly progress.

What has been said so far applies only to seed from stands within the natural range of the tree-species. It must not be overlooked that we also have examples of tree-species which exist under conditions such that they have been moulded by man's intervention, and the effect of this may be so strong that it has become possible to speak of types which have evolved in this way. As examples of this, reference may be made to Douglas fir in Scotland and to the avenues of oak in Holland, while we in this country also have an example in a peculiar, small-coned type of European larch.

To take the last case first, for which we have the oldest data, the history is as follows. About the year 1800 there came to Denmark a sample of larch seed from eastern North America. The trees raised from it still form a fine, but rather slow-growing, group or small stand. They have distinctly small cones, and because of their origin they have been regarded as being of original American ancestry. Historical investigations, however, seem to make it much more likely that they owe their origin to JOHN BARTRAM's introduction of European species to the region around Philadelphia about the year 1750. Everything so far known indicates that here we are concerned with an instance, where a European forest tree has been isolated for the past two hundred years in North America, from where we brought back a small-coned " type " a hundred and fifty years ago.

From his headquarters in Fort Vancouver beside the Columbia River, DAVID DOUGLAS despatched the first small sample of seed of Douglas fir to Europe in 1826. Two trees from this happened to be planted at Scone in Scotland, and as early as 1873 it was computed that the yield of seed from these two trees and their offspring up to that time had furnished about three million plants. On the estate and far beyond it this tree-species had thus become quite widespread through the existence of these two trees—and of the inherent tendencies which they alone contained—before it became the usual practice to import seed through seed-merchants. In that way had evolved a several times home-bred "Scone-Douglas" remarkably suited to the site. This was done by man's intervention and it cannot be likened merely as a matter of course to normal progeny from the original region, although the two trees are quite different in appearance from one another. After visiting both places it is my impression that the Douglas fir at Scone is of a more homogeneous character than the progeny in the natural stands. The old stands at Fort Vancouver have long since been felled.

Regarding the example of the oak avenues in Holland the following may be mentioned. It is now very general in Denmark to prefer seed from the Dutch oak avenues rather than the seed from our natural oak stands, and as the result of more than half a century of experience, by doing this we get a finer and more straight-boled progeny. It may have been a better type from the hand of nature that has been used in planting the avenues in Holland and Belgium. Part of the reason seems to be that, in the planting of these, which goes back to about the year 1800, the better trees have consistently been selected, and that in all cases the smallest trees have naturally been avoided. In any event a very characteristic type has been obtained, in the genesis of which the intervention of man can by no means be excluded. It may also be a pointer indicating that even a quite simple selection is capable of characterizing the progeny.

It is very probable that a more intensive study of the process of introduction and form of the first cultivation of forest trees under strange, isolated conditions may have considerable value for assessing the utility of our cultivated tree-species. An approach to " cultivated types " may occur. It is most important that by progeny trials and assessment of the value of the species in cultivation we should be on the look-out for their possible appearance.

That is a problem which not only concerns the true alien tree-species (exotics), but is of importance in the general movement towards promoting certain desirable species at the expense of others.

CHAPTER IV

CONTROLLED POLLINATION

By far the greater number of forest trees have their female flowers pollinated through the help of the wind. Here in the north that is true of all our forest trees; throughout the globe it applies to all coniferous trees and to a large part of the leaf-trees. As regards the remainder, it is left to the insects, who pay just as little heed as the wind to forest economics.

We know to-day, and for that matter it has long been known, that the rate of growth and the quality of the trees depend not merely upon the soil and the external conditions under which they grow up. The energy with which the tree grows, its branching, stem-form, resistance to frost and disease, even the actual anatomical structure of the timber and all those other things which together go to make the good or poor tree, are also determined by its inherent tendencies. Much in the same manner as we human beings and all other living organisms of both the animal and the plant kingdoms are graced or endowed with different characteristics through sexual reproduction, so is there great "congenital" variation within the individual tree-species.

We know, further, that the inherited characteristics of the offspring are determined to an equal extent by the female and male elements, which have constituted the individual's parents. The female element, the seed from the individual tree, may readily be controlled, but the position is quite otherwise with the male element, especially when it is the wind that spreads millions of pollen-grains abroad over the female flowers of other trees. In the "progeny trials" usual in forestry when we have employed seed from selected outstanding trees, we have always used seed which has been produced after free, uncontrolled pollination. As it must be presumed that it is by far the most common occurrence that the seed of a tree develops after outside pollination, while laying emphasis upon our having control over the mother, stress may also be laid on the fact that we know nothing of the father.

Such progeny trials are by no means without value; we must understand clearly that there is a limit to what we are entitled to conclude from them. We should have a far sounder basis if we worked with progeny from controlled pollinations, in which we knew both the mother and the father.

In agricultural and horticultural plant improvement it has for long been of decisive importance to work with controlled pollinations as a link in efforts at improvement. This has played a very important part in the brilliant results within these land-uses in respect of crop-yields, which far exceed the production of earlier times. It is only the fact that the trees often do not flower until late in life, when the female flowers are very inconveniently placed for isolation and controlled pollination, that has, presumably, been the cause of silviculture's primitive status in this field.

It is just this flowering of the trees late in life that is the cause of the slow succession of generations, which makes it very necessary to take the best advantage of every means of obtaining the most reliable basis for our conclusions.

In deliberately undertaken improvement work we must not retreat before the seeming difficulties of controlling the pollination as a basis of our future progeny trials. Nor is it so insuperable to put it into practice, and when it is *combined with vegetative propagation* of the selected trees, it can be done cheaply and carried out on a considerable scale. For the economically important coniferous trees and a number of other important forest trees there is a great advantage in the female flowers being grouped together into larger inflorescences. Besides, they bear abundance of pollen which can be easily gathered and kept for a sufficiently long time in a state available for artificial pollination.

The whole work has, however, a distinctly botanical character and one has to operate with great accuracy. First of all one has to become acquainted with the manner in which female and male flowers are distributed in the case of the individual species which it is desired to work with. Next, one must be prepared to show a considerable amount of self-reliance in planning and carrying out the work, for experience is limited, and many details have to be fitted together.

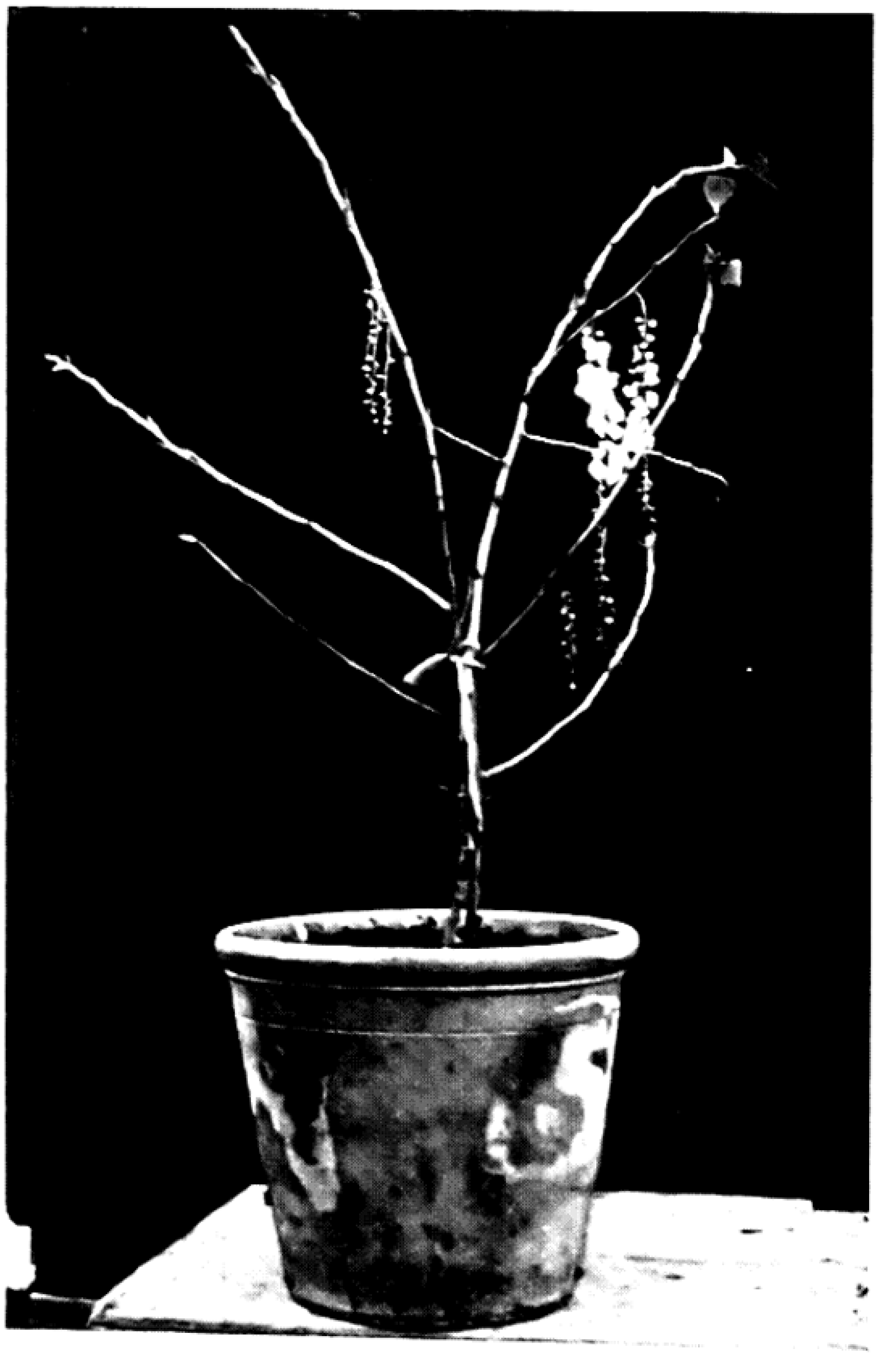


Fig. 6. *Populus nigra* L. Scion cut from female tree on 1st February. Placed in water in a warm room and later planted into moist peat. Pollination on 15th February. *Photo.* 5th April 1939.

Poplars have been great favourites in improvement, because in cultivation spontaneous hybrids readily arise between them, and also because of their easy vegetative propagation by cuttings. In the more recent improvement work, which operates with controlled pollination, they have also shown conspicuous advantages. Poplars constitute a distinctly diœcious species with female trees and male trees; moreover, the male catkins produce large quantities of pollen, and the female trees have inflorescences, each of which contains a large number of female flowers and can therefore furnish many seeds from the individual catkin. The Austrian WETTSTEIN was the first to utilize the capacity of the poplars to set viable seed on cut-off branches. The cut-off branches permit of being handled like ordinary cut flowers in a vase, and they can be admitted for use in controlled pollination in that simple manner and both female and male flowers can be brought into use while they are still at the bud stage, after which they can be induced to flower and furnish pollen, and later to continue their development and bear ripe seed.

This is an example of the easiest form of controlled pollination. In a small greenhouse only a few yards square, or even in a room, one can produce in that way controlled seed of poplars giving thousands of plants. The method is employed in Denmark for the commercial production of the hybrid between *Populus tremula* and *P. tremuloides* (European and American aspens), which is so valuable to us.

In other genera, such as *Juniperus* (juniper) and some species of *Fraxinus* (ash), we have the same advantage of the uniform segregation of the flowers to female and male plants. Although in these cases we cannot use the cut-off branches for seed production, nevertheless the location of the flowers implies the great advantage that it is easy to exercise control over the individual sexes.

By far the largest proportion of forest trees, however, have female and male sexes on the same tree, but nevertheless in such a way that the two sexes are found separated into female and male flowers. The more complicated state of affairs in which we can speak of an emasculation of the individual flower can almost be left out of account. Where removal of the stamens from the individual flower is required, it must be done very carefully and may be quite difficult, but it is of such small importance in the case of forest trees that it will not receive further mention here. Information about it must be sought in the general botanical literature.

On the whole we can confine ourselves only to the case where we have flowers of separate sexes growing dispersed over one and the same tree and we also have the great advantage that the flowers of each sex are in most cases found growing together in special inflorescences, which are much more easy to control.

Very often the inflorescences of the female and male elements respectively grow scattered promiscuously, though with *Abies*, for example, each may grow so as to be more restricted to its own part of the tree. *Abies* has the female inflorescences growing grouped around the top of the tree, whereas the male flowers grow lower down. As the female and the male inflorescences are, moreover, very different in appearance even when in bud, it is particularly easy in this case to isolate the female flowers. *Larix* (larch) may be taken as an example, in which it is not at all easy to recognize the difference in the two sexes when they are still in the early bud stage; on the other hand, it is very easy shortly before flushing. This means that in such a case one has to work rapidly in the relatively short time which may be available.

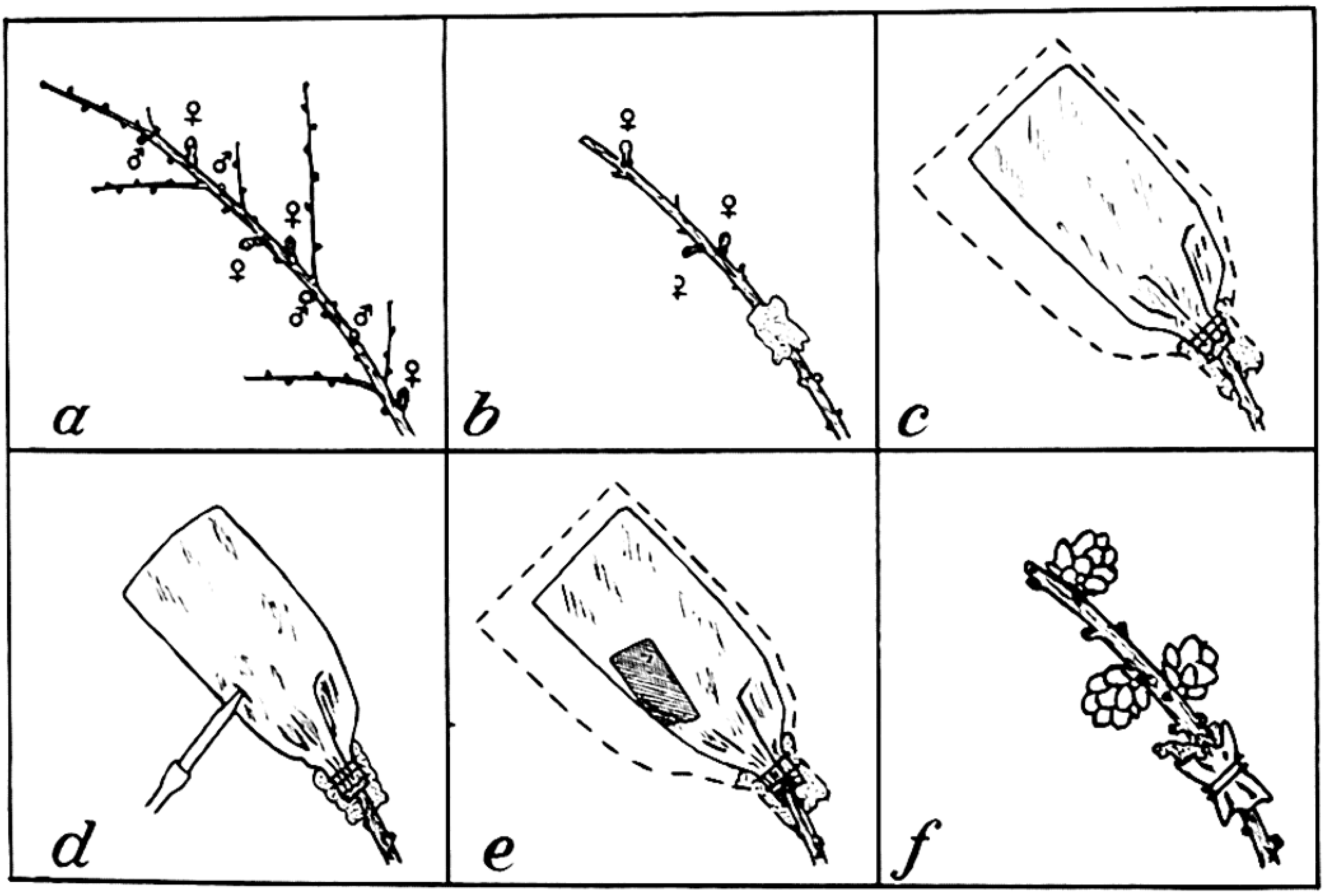


Fig. 7. Pollination artificially performed (*see* explanation in text, p. 46).

In the case of the genus *Fagus* (beech) we have an example in which it has been difficult to carry out isolation without mistakes. Here we certainly have a distinct advantage in that the two sexes occur in separate flowers, but, after removal of the male flowers, now and then occasional male elements may appear which, being very small, have been overlooked and which after isolation have developed further. In such a case it is particularly necessary to make a careful re-examination for males which may possibly have been overlooked when bringing down the isolation material. These are only some examples drawing attention to the very varied conditions which may happen to arise when working with the individual species. As already mentioned, the work requires self-reliance and care.

Of decisive importance for controlled pollination is the timely isolation of the female flowers. This must be done so early that the female flower or the whole inflorescence with the female element is still in the bud stage, and in any event has not begun to unfold.

The method of procedure is illustrated in Figs. 7 and 8. From branches with buds of inflorescences of female and male flowers respectively, the latter are removed, while at the same time any excess of small twigs is cut away. A small strip of waterproof cotton is fastened round the branch, with the buds containing female flowers now remaining isolated. (7 (*b*)). Two transparent parchment bags of different size are then used. They may, for example, be 13 × 26 and 17 × 31 cm., and they must be examined to see that they are satisfactorily gummed along the joins. The smaller bag is inflated and placed over the twig, so that it can be attached to the belt of cotton already fixed in position. The union is carefully closed again with a fresh strip of waterproof cotton, and the larger bag is drawn over for further protection (7 (*c*)). With us it is a good plan that the interposed wadding should

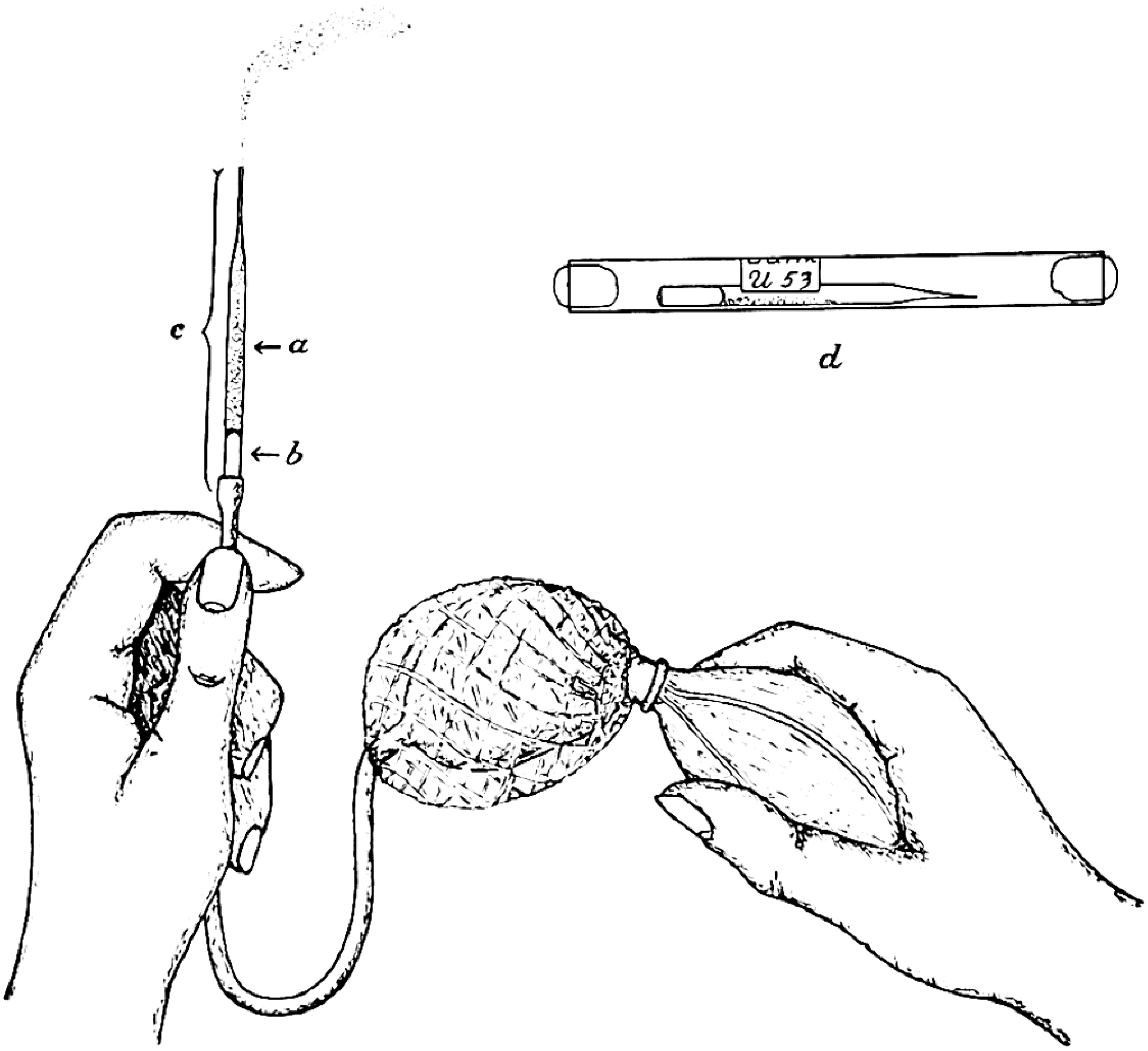


Fig. 8. Blower used for inserting pollen into the bags.

be completely covered by the outer bag. Otherwise, birds will remove it for nest-building and while working to get it loose may also cause damage to the bags.

When the flowering commences, the outer bag is removed, so that through the transparent wall of the inner bag one can form an opinion as to whether these flowers are ready to receive the pollen. If they are ready the desired amount of pollen is introduced by means of the blower shown in Fig. 8.

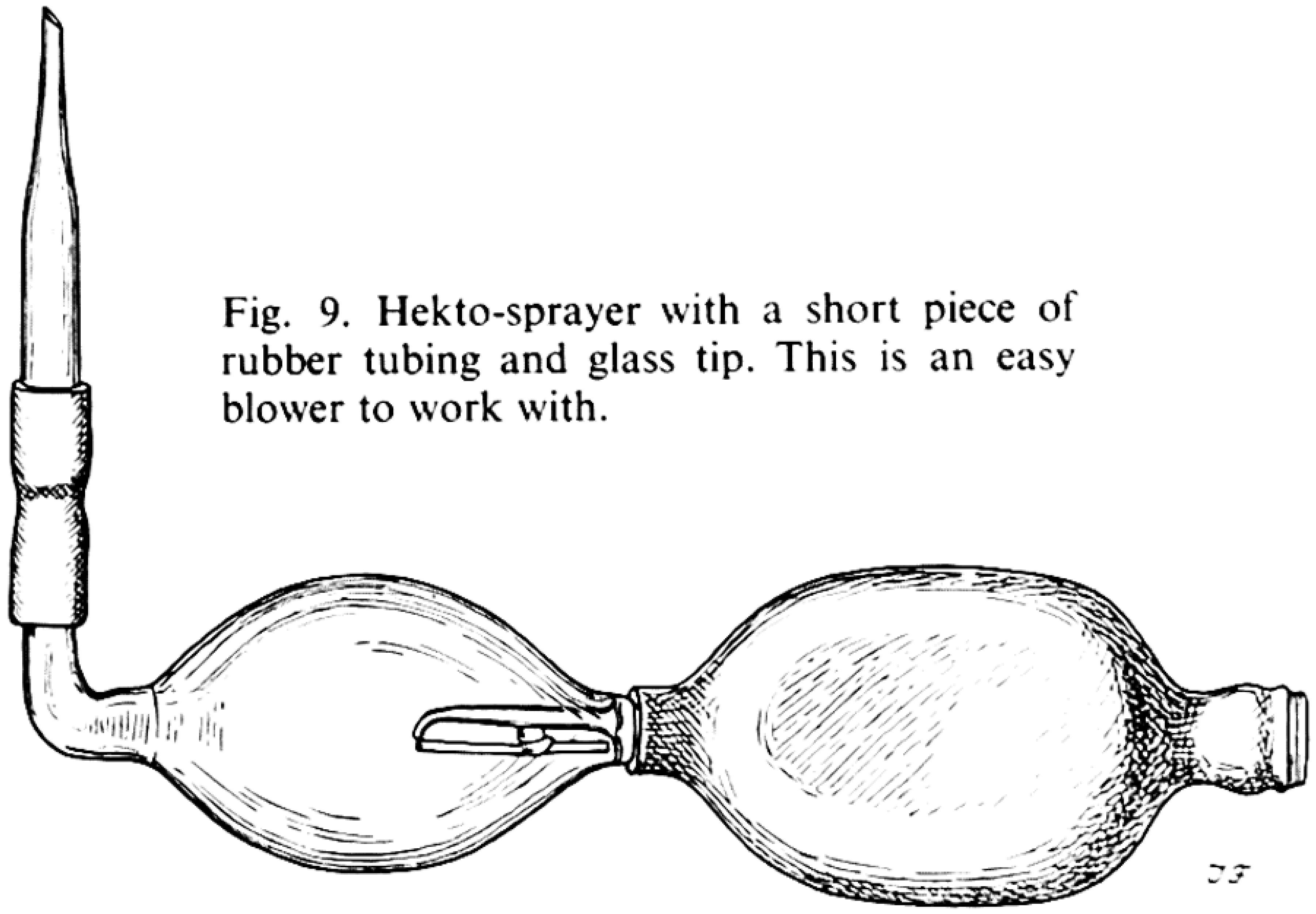


Fig. 9. Hekto-sprayer with a short piece of rubber tubing and glass tip. This is an easy blower to work with.

The glass tip is thrust through the wall of the paper bag, and by careful pressure on the blower a thick cloud of pollen is scattered over the isolated female flowers. With favourable light conditions this process may be followed through the moderately transparent wall (Fig. 7 (*d*)).

The small cotton-wool plug (Fig. 8 (*b*)) prevents the pollen (*a*) from dropping back into the blower. At the same time it is only necessary to remove the glass tip (*c*) when changing to another pollen. The glass tips with pollen are kept protected in glass tubes, the ends of which are closed with cotton-wool plugs (Fig. 8 (*d*)). Glass tubes and glass tips are so cheap that, if desired, they can be broken after use in order to prevent any chance of defective sterilization.

Another more practicable " blower " is the Hekto-sprayer used by asthmatic patients, which is illustrated in Fig. 9. It is handy to work with and easy to sterilize.

After sufficient pollen has been conveyed to the female flowers, the glass tip is carefully withdrawn, and the hole produced is closed over with a securely adherent strip, of Scotch tape, for example. The outer bag is replaced and the controlled pollination is accomplished (Fig. 7 (*e*)). When the inflorescence has closed up, or when one has made sure, in some other manner, that there is no possibility of further pollination, both bags are removed. At this dismantling the isolation material is carefully checked for remains of male flowers which have possibly been overlooked and for injuries. If there are remains of male flowers, or holes are discovered in the inner bag, the pollination must be rejected. One should work with caution, but on the other hand not allow the isolation material to remain in place unnecessarily long.

What has been described here is the simple form of carrying out controlled pollination. In this manner it can be done cheaply and with primitive aids, provided the work is performed carefully. For more than twenty years it has been the procedure generally applied in Danish forest-tree breeding. I have preferred to work with simple and cheap methods, which nevertheless provided me with the means for frequent repetitions, and this seems to me to ensure the best form of reliability.

It is not astonishing, however, that at Placerville, California, they should have preferred to do the isolating with more solid bags. There they work almost exclusively with *Pinus* (pines), the majority of whose species have particularly long and sharp needles.

At the Institute of Forest Genetics at Placerville they use for isolation of the female flowers of pines strong canvas bags with plastic panes, which permit of accurate observation of the flowering. At the time of pollination these are carefully pierced with a glass tip bearing the pollen. After use they are carefully sterilized, so that they can be used year after year.

"Cellophane" and plastic material present opportunities for a better technique in isolating the flowers. The smaller penetrability of the completely transparent material by the air has in this case to be offset by special precautions. A satisfactory solution has been reached at the Danish State Forest Plant Breeding Station, where in recent years plastic tubes have been used.

There they use a tube open at both ends, which is made of stiff and strong plastic, measuring 30 cm. long and 6 cm. in diameter. The appropriate branch with the isolated female flowers growing upon it is pushed up into the tube, which is closed towards the tip with a perforated layer of plastic. This is further covered with a layer of waterproof cotton and a piece of gauze, which is fastened down over the rim of the tube with an elastic band, which is furnished with a tag. When carrying out the pollination the covering layer of cotton is carefully loosened by pulling on the tag and the pollen is conveyed by means of a glass tip and it is then closed up again. Underneath, the plastic tube is stopped up with waterproof cotton, after an appropriate band of needles has been removed, so that it can be tightly closed. A few holes on the lower edge of the tube make it possible to fasten it solidly to the branch.

This is a good method, which makes it easy to observe the flowers during the progress of the work, while it is also a better protection against pressure than the less rigid bags and so is specially to be recommended where there is a risk of the destruction of the paper bags by rain and wind.

The other part of the process, consisting of the collection, cleansing and storage of the pollen, presents no great difficulties as a rule. The greatest reliability is attained by cutting off branches even before the flowers begin to produce pollen and by placing them in glass isolation chambers adapted for the purpose. If the branches are put into water, and the male flowers are then subjected to appropriate warmth and dryness, they will usually readily cast their pollen. Impurities can be gathered up from outspread pieces of paper right away. It is easily cleaned by shaking it carefully through a piece of gauze and with the help of a piece of folded paper it is introduced into the glass tips (Fig. 8. (*d*)) so that it is ready for use. Every time one proceeds to deal with fresh pollen, the hands must be washed, all paper which has been used destroyed, and every precaution taken to avoid unwanted pollen. At the State Forest Plant Breeding Station, improvements have also been made in this procedure by arranging for a direct absorption into the glass tips through gauze, which keeps back the impurities. This can be done with an ordinary vacuum-cleaner and works easily when the pollen is not too impure. It should thus certainly be possible in one way or another to do this both more easily and with steadily greater reliability. The latter point is the more important and will continue to be so.

It is easy to preserve the pollen during the current flowering period, when it is a question only of weeks or perhaps as much as a month or two. It has only to be kept dry and not subjected to too great fluctuation of temperature. One example of pollen, which can be difficult to preserve even for a few weeks, is *Fagus* (beech). In this characteristic it is reminiscent of *Hevea* (the rubber-tree), with which one seems to experience similar trouble. In such cases it may be a question of using " fillers ", such as talc or light, dry pine pollen, as it is particularly easy to work with pollen of *Pinus* (pine) and other conifers. A report from Placerville exists of quite successful preservation of pollen from *Pinus* for ten months. This is a subject in which further research is much needed, as it would be very helpful if pollen could be preserved over longer periods of years as is done with different kinds of tree seeds. In that way there would then be an opportunity to set up a " pollen-bank " similar to the " blood-bank " of a hospital, and this might be expanded into an organization for the exchange of pollen on the same basis as that for the existing general exchange of seed between research stations.

It seems to me that there may be great possibilities in this connection for further inquiry in support of the general development of forest-tree breeding. The matter must be looked at in combination with the fact that, while several of our economically important forest trees produce large quantities of pollen, there may also, on the other hand, be some years between times of flowering and thus between opportunities to collect the pollen. When we possess the pollen it is easy to transmit it. It goes with perfect safety by ordinary air-post; small amounts need only be collected in a piece of paper and inserted in an air-letter. For years we have used this method without mishap, and it is a great convenience when " the father " can come flying by post.

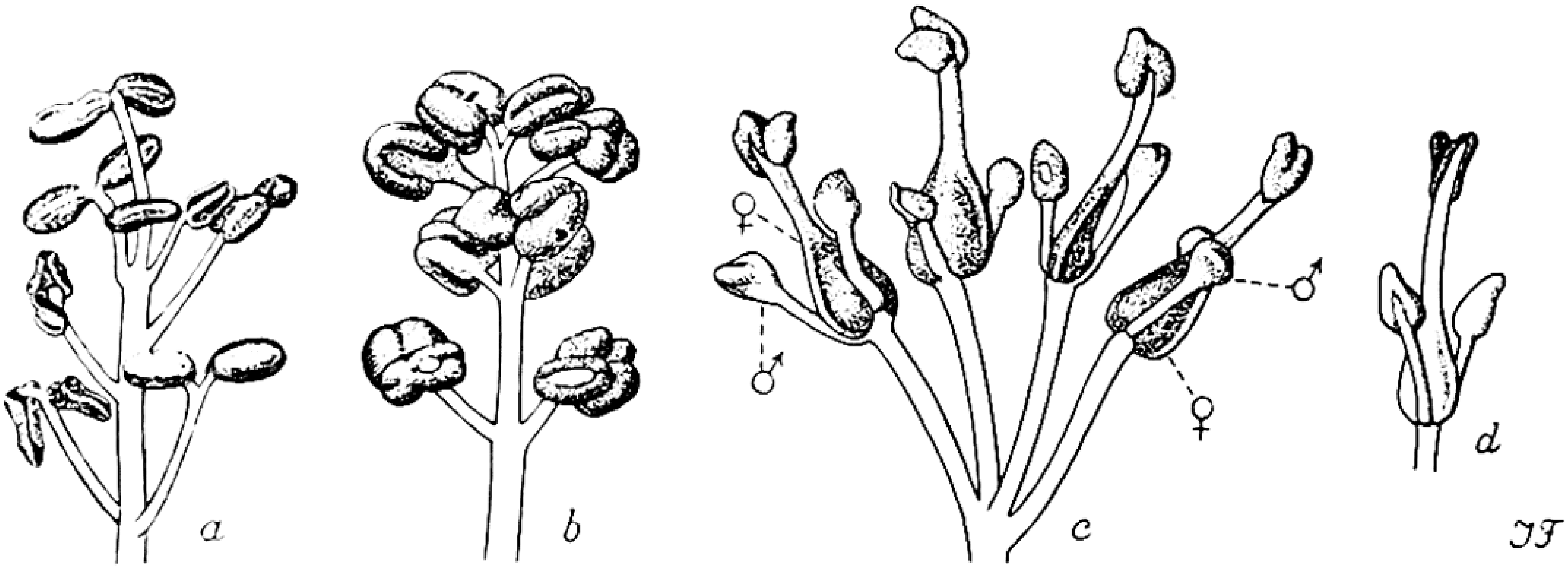


Fig. 10. *Fraxinus excelsior* L. Flower types in ash; April 1943. (a) and (b): Male flowers; (a) has open and (b) has closed pollen sacs. (c): Bisexual flowers. Ovaries (♀) in growth (pollinated), and the anthers (♂) still closed. (d): Female flower with rudimentary appendage.

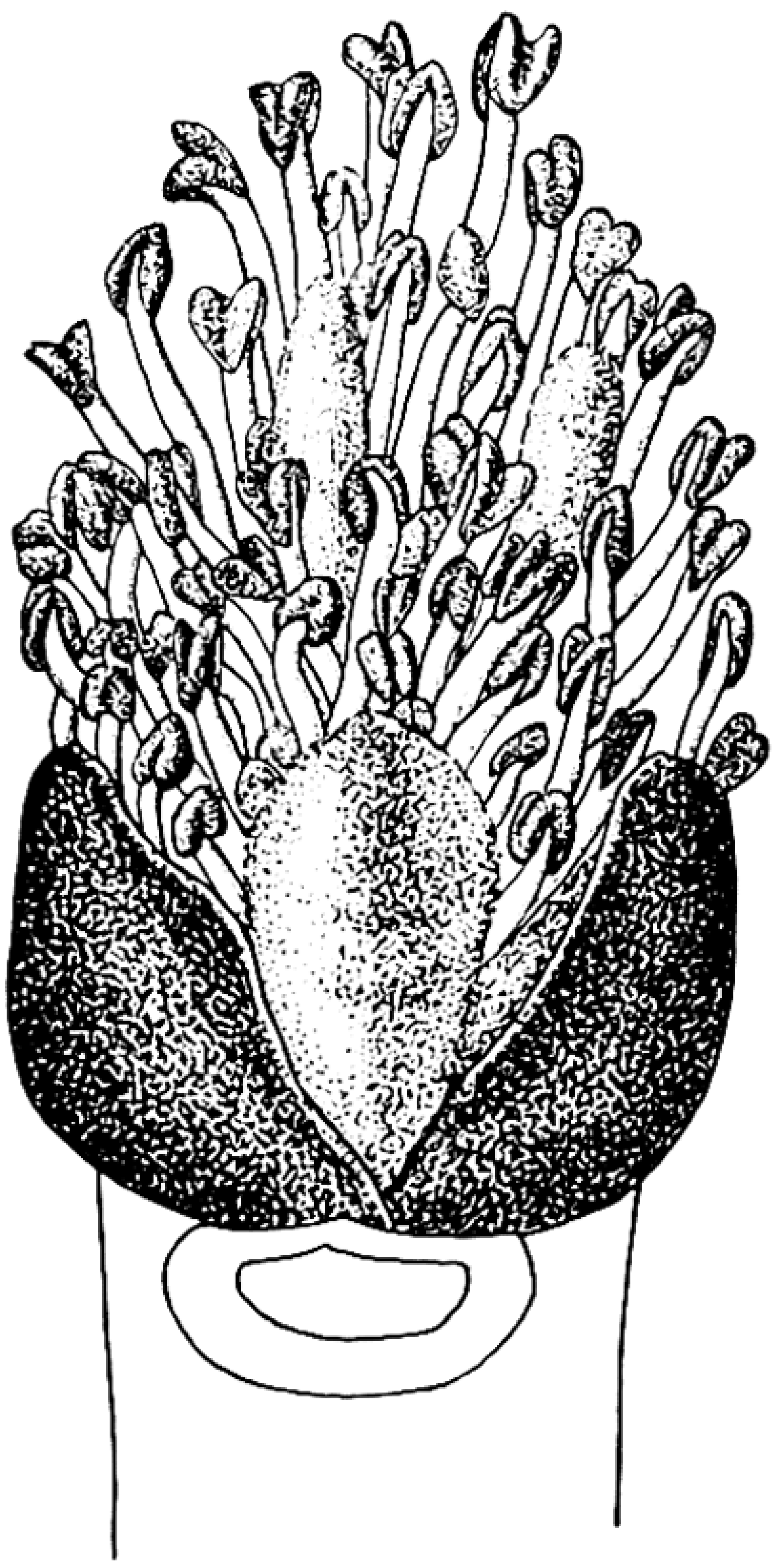


Fig. 11. *Fraxinus excelsior* L. Purely female inflorescence in bloom; April 1943. The female flowers are ready to take pollen immediately after the bud-scales have expanded.

Associated with the problem of preserving the pollen there is the question of procuring it in time. Many species permit of being brought on by means of cut-off branches, so that branches can be taken into a greenhouse for such early treatment that pollen can be secured at the right time. Moreover, the flowering of those species and individuals, which it is desired to work with, must be followed from year to year. Not only are there differences in flowering time between the various species, but even between individuals of the same species.

This may to some extent be due to the growth-site, or it may also be of an hereditary nature, but whether it is due to the one cause or the other we must endeavour to plan the controlled pollinations in the best possible manner for utilization of the pollen. Usually that will mean that we arrange to permit the female flowers on the late individuals to be pollinated with pollen from the earlier ones. It all depends, however, on the abundance of the female and male flowers, and the sequence in time of the behaviour of the two sexes, not only from tree to tree, but also on the individual tree. While the flowers are developing, rapid decisions must often be made, as it will not always be possible to follow a pre-conceived plan.

As previously mentioned, with some species there is such a marked discrepancy between the two sexes that there are trees which are either male or female, and as an example the poplars were mentioned. Even in such cases there may arise as rarities individuals with both sexes on one and the same tree. TH. MEEHAN reports such "a monœcious case" in *Populus tremuloides*, and in our Forest Botanical Garden here we have a *Populus lasiocarpa* with both female and male flowers. Moreover, it even furnishes an abundance of plants when its seed is sown.

In the case of a genus like *Fraxinus* (ash) the matter is more complicated. In it, it is reported that there are a number of species, especially American, that are clearly differentiated into individuals, which are either female or male, whereas *Fraxinus excelsior* (the European species) is more variable. In it are certainly found pure female trees and pure male trees, but also trees with both female and male flowers and even bi-sexual flowers. With the economically important forest trees, however, it is most usual to find female and male flowers on the same tree, in such a way that they grow in separate groups in the form of pure female or pure male inflorescences.

In carrying out very intensive work with rather a large number of individuals of a single species, it is often possible to observe a variation in the proportions of the quantities of flowers of the two sexes. It seems that to some extent this might be affected by external conditions or be determined by the age, but there also appears to be an hereditary factor taking part. Some individuals may be more markedly feminine and others more masculine, although they belong to the same species normally described as monœcious. I have dealt with this in more detail earlier in "The Employment of Species, Types and Individuals" (*Royal Veterinary and Agricultural College Yearbook, Copenhagen*, 1937, pp. 46–9).

There is a tendency to notice only the markedly feminine trees as being particularly " fertile ", so it is easy to overlook the individuals accentuated in the masculine direction, which nevertheless, because of the marked abundance of the pollen they produce, may have had just as much significance in respect of the collective progeny of the stand as even the most heavily seed-bearing tree. Both sexes are of equal significance in breeding, so that early attention must be devoted to this matter.

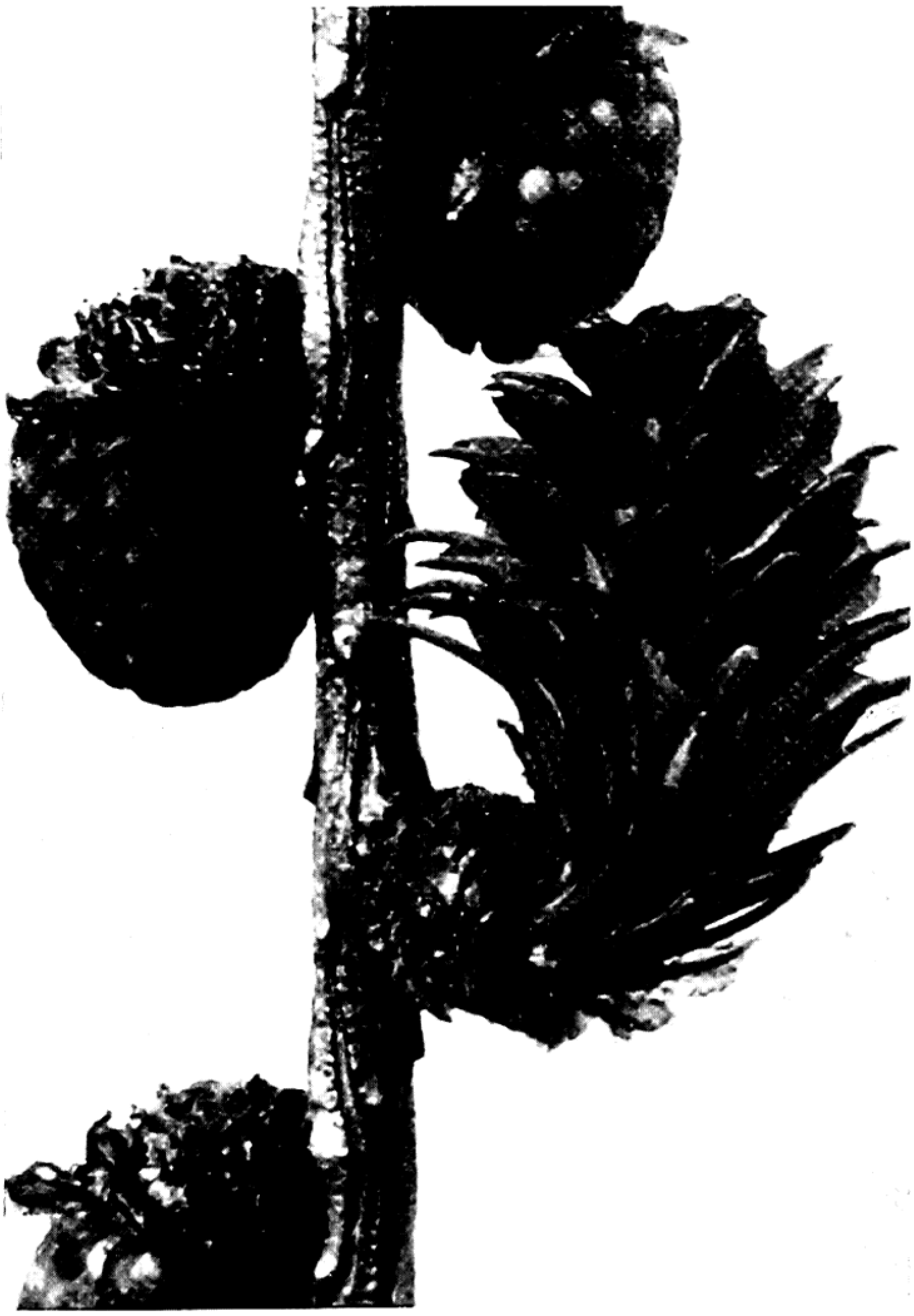


Fig. 12. *Larix decidua* Mill., 28th April 1936. The female flower open and accessible to pollen, whereas the male flowers are still closed; metandry.

It is important in addition to observe the time sequence of the two sexes of flowers on the same individuals. There is a characteristic tendency for female and male flowers on the same tree to begin flowering at different times. If the female flowers appear first, this is known as metandry (protogyny). When the opposite occurs we speak of protandry (metagyny). I have dealt with this question previously (loc. cit., 1937, pp. 58–67), and come to the conclusion that, for a long list of forest trees, metandry is a general feature of their flowering. With a genus like *Abies* (silver fir) it is so pronounced that the female flowers may be open for fertilization more than a week before the tree's own male flowers are able to shed their pollen. In other cases it is a matter only of days.

Nearly twenty years have passed since this statement was made, and later experience strengthens me in the opinion that it is true. There are many exceptions, but metandry is so common that in most cases it is not very difficult to find that feature in those individuals which are also endowed with outstanding forestry qualities. Pronounced metandry seems to me to be of great value in breeding. It is therefore important to have it determined for those trees selected for breeding stock.

When carrying out the isolation before the controlled pollination it is an advantage to have these early female flowers. They are easy to recognize, and inconvenient, neighbouring, male flowers, perhaps on the point of producing pollen, can be ignored when the female flowers are being identified. For subsequent use in breeding by means of " seed-gardens " it is of the greatest importance, because a metandrous tree, in the days which pass between the time the female flowers become receptive and that when the male flowers begin to produce pollen on the same tree, can be regarded as a purely feminine individual. During those days it will be receptive of pollen brought from elsewhere, so that the pollination can be carried out in a certain desired direction.

On this subject of the biology of flowering a great deal of work is still required, and it is to be hoped that the work will be taken up, as soon as its importance in the breeding of seed for forestry becomes more generally recognized. It ought to be an attractive task for the forest botanist, for it involves interesting biological problems. The American TH. MEEHAN writes as follows in the article " Contrib. Life Hist. in Plants, 3: Dichogamy and its Significance " (*Proc. Acad. Nat. Sci., Philadelphia*, 1888, p. 391): " Among the contributions I have made to botanical science, few impress me with more importance than determination of the fact that a degree or measure of heat capable of exciting the male organs to grow, may yet be wholly inadequate to start growth in the female." Somewhat later, MEEHAN drew attention to the importance of nutrition in the formation of female and male flowers (*Proc. Acad. Nat. Sci., Philadelphia*, 1899, pp. 84–86), while it has also been referred to by KENJIRO FUJII (KNUTH: *Handbuch der Blütenbiologie*, Vol. 3, 1904, p. 40). Nevertheless, continued investigations into this problem, which is so important for us, still remain to be done.

For every operation in controlled pollination it is necessary to work with a lens, as one must be able to decide with accuracy whether the female flowers are open and receptive of pollen. It is not good enough merely to apply the pollen " in good time " and then hope that the pollen-grains will reach the female element at the proper period; all too often the applied pollen then remains clinging to other parts of the plant or coalesces and becomes unserviceable. Before the pollination the female flowers must be closely examined and one should make sure that they have the right development.

The female inflorescences of the coniferous trees, which later on develop into cones, may be a little difficult to appraise. They must be dealt with while the carpellary scales are freely parted from one another, so as to allow unhindered access of the pollen in between the scales to the exposed ovule. In order to be sure of a thorough pollination it may be necessary to repeat the application of pollen in the hope of finding the female flowers at a slightly different stage of development.

Growing in the open on the tree and exposed to general pollination there is usually a very short time during which the female flowers are receptive to pollen. The position seems to be somewhat different in the case of the isolated female flowers, where in some cases it has been found that there is a waiting period for arrival of the pollen. Under such circumstances the virgin stage may be not inappreciably prolonged. This may be a great help at a busy time, but the course of the flowering must be carefully followed so as not to over-estimate it.

The description given here of controlled pollination is prefaced with an observation to the effect that it has long been known that the inherited qualities of trees are of great importance. Likewise it is stressed that it is of great significance to have control over both sexes in order thereby to be able to contribute to the elucidation of these important matters. One might imagine from that, that there had been a great deal of work in that field.

Work has been going on for a long time, but there has not been much progress until recently.

The oldest known instance of controlled pollination of forest trees was carried out by KLOTZSCH about 1845 (KLOTZSCH: *Nutzanwendung der Pflanzen-Bastarde und Mischlinge*, 1854. Reprint in the Central Botanical Library, Copenhagen, origin unknown). He made use of it in producing hybrids in, amongst others, the *genera Pinus* (pine), *Alnus* (alder), and *Ulmus* (elm). In 1877 it was used by LUTHER BURBANK in his species crossings in *Juglans* (walnut), and although the result of the experiments in both cases was very promising, we pass right on to 1912 before controlled pollination was again employed to produce a hybrid for forestry. That was AUGUSTINE HENRY's *Populus generosa*, which he produced by pollinating *Populus angulata* with *P. trichocarpa*.

In contrast to KLOTZSCH and BURBANK, HENRY had an easy way of fixing the product of his crossing by vegetative propagation for further use in practice, and it attracted considerable attention. Controlled pollination in poplar was later undertaken in an extended form in the U.S.A., where STOUT, SCHREINER, and MCKEE did further work by making isolations and pollinations of poplar in the New York Botanic Garden. W. VON WETTSTEIN-WESTERHEIM improved the method at the Kaiser Wilhelm Institut für Züchtungsforschung in Germany, and obtained good results with a method, very simple to apply for that genus, of operating with cut-off branches in a greenhouse.

In 1909, N. SYLVÉN used controlled pollination for carrying out self-fertilizations of *Picea Abies* (Norway spruce) in order to obtain material for comparison with progeny produced by free pollination as a basis for investigations into types of branching. At the " tree-breeding station " established at Placerville, California, in 1925 (the forerunner of the present " Institute of Forest Genetics "), it was later employed to produce hybrids of *Pinus* (pine), and A. DENGLER also used it in his valuable research with *Pinus sylvestris* (Scots pine), the results of which he published in 1932.

In our Forest Botanical Garden here I carried out in 1924 the first controlled pollination, by which I obtained promising progeny of *Abies grandis* × *Lowiana*, and in 1930 I took it up on a larger scale especially with *Larix* (larch). I gave a report on that in *Forest Tree Breeding* in 1934.

There is great fascination (and it gives a very valuable insight into the process of flowering) in being able to clamber around in the trees oneself and undertake the pollination. I also erected scaffoldings of various forms in order to be able to make the controlled pollinations more conveniently and on a larger scale. This is a difficult task, however, and it is therefore not surprising that I was soon converted to the use of vegetative propagation as a technical aid in forest-tree breeding.

By means of graftings, cuttings, or other forms of vegetative propagation we can mould the desired trees into a form suitable for the work. In that way the breeding proceeds in a very different and more ambitious fashion. It becomes, as it were, " rationalized ", and since our first successful graftings were made in the spring of 1934, it has steadily developed hand in hand with the extended use of controlled pollination.

It is not only the appreciation of the need for controlled pollination in investigations into the effect of the genetic factors, which has brought new life into forest-tree breeding. This must also be attributed to the use of vegetative propagation, which makes the work practicable and opens out the prospect of being able to make use of the accumulated results in practice. The two problems must therefore be looked at together.

CHAPTER V

VEGETATIVE PROPAGATION

WHEREAS in the reproduction of trees from seed an alternation of generations takes place, in vegetative propagation we can speak only of a simple division of the original individual.

Populus nigra var. *italica* (Lombardy poplar or pyramidal poplar), which is widespread in Europe, was already a feature of many settlements in eastern North America about two hundred years ago. This tree, which is so characteristic a feature in any landscape, now occurs widely in California, New Zealand, Australia, South America, and many other places around the world, and these are *all parts of one and the same tree.* Wherever men went off to make settlements, they took twigs (cuttings) along with them, stuck these in the ground, where they struck root and grew up to be trees with precisely the same qualities as the tree from which they had been taken. This is propagation by division from tree to tree and a typical example of vegetative reproduction. It is the same procedure which is utilized in the propagation of potatoes and fruit-trees, and in the cultivation of bulbs, roses, and many more of our common cultivated plants.

In the case of a succession of generations, in which the progeny are produced by sexual reproduction from seed, a new individual is formed, since it acquires inherent tendencies from both the " mother " and the " father ". In the kind of reproduction in which only a part of one tree grows on as an independent plant, the new plant will contain exactly the same inherent tendencies as the original. It possesses the same content of inherent tendencies (genes), whether it is a piece of the root, a twig, or a bud which is in a position to grow on into an independent individual.

In vegetative propagation we perpetuate the hereditary constitution existing in a tree, whereas, because of the succession of generations in sexual reproduction, new plants are raised with a different constitution (selection) of inherent tendencies.

With the help of controlled pollination between good parent plants we can supply ourselves with the best possible initial material, and hope for steady progress, but because of the slow succession of generations this is rather difficult in forestry, where we are used to waiting for twenty to forty years for the natural seed-setting of a tree. In agriculture, in which every year or every other year there is a sexual generation, it is possible to arrive much earlier at an improved progeny by continued selection of the plants giving the highest yields. This process has been used on a large scale and has given brilliant results in both agriculture and horticulture.

The progress by means of this method with herbaceous plants has been so overwhelming that from the silvicultural point of view it has been viewed with envious glances and then renounced. Thoughts were directed only upon the number of generations and the very long, almost interminable, time which would have to pass before anything similar could be done for forestry. We simply must not despair; all we have to do is to follow another path. First of all we should try to comprehend the enormous advantages we have when we work with long-lived individuals.

When the farmer finds a high-yielding individual, whether it be a cow or a turnip, it dies as far as he is concerned in the course of a relatively short time. He cannot cut off the hairs or ears of the cow and thus obtain several cows with exactly the same qualities. He can only hope to get something similar by parturition.

If we discover an outstanding tree, in the first place it lives a long time; but, in particular by vegetative propagation, we can move it and bring it into a form which is convenient for the breeding of seed, and incidentally can keep it alive as long as it suits us. That will usually mean until we have found something better.

Before we develop improvement work to raise something better than is known to-day, there are good reasons for first of all making sure of the best from that which nature has provided. That this will already imply a great deal can readily be appreciated by observing the great variation in trees of the individual species.

The flowers of trees are often so inaccessibly placed, high up, that it may certainly be desirable to have them changed over on to smaller plants, on which the flowers are conveniently placed for controlled pollination, but at the same time retain the inherent tendencies absolutely unaltered.

Vegetative propagation can take the form of grafting, budding, and cuttings, or more ingenious operations, in which, however, there is always a vegetative part of the original plant which is capable of independent development.

This is a particularly important technical aid in the work of improvement in forestry, because it gives us the opportunity to preserve the desirable trees as living individuals for as long as there is a use for them. Furthermore, we can move them about very much as it pleases us, and they can help us towards a greater and more speedy yield of seed, even after being the subject of an appropriate pollination. *It ensures that there is no regression*, because we can retain the most valuable trees in the forest as living specimens. It allows us to change the location of these trees, their external form and size, so that, without changing their inherent tendencies, we can bring them into a convenient form for use in *controlled pollination on a larger scale.*

It gives us series of genetically identical material for *analysing the inherent characteristics of the trees.* These comprise, for example, growth-energy, stem-form, branching, resistance to frost and sickness, biology of flowering, etc. (cf. the chapter on " tree-shows ").

It provides us with *whatever number of genetically identical plants we may require*, which can be planted out for pollination as desired, and thus allows us *to breed the appropriately fertilized seed in the quantity desired* (cf. the chapter on " seed-gardens ").

In vegetative propagation we distinguish here only between grafting and use of cuttings, so that to *grafting* belongs budding, and under *use of cuttings* are included both woody and herbaceous cuttings and cuttings from roots.

It is a feature of grafting and budding that we employ " foreign roots ". In grafting a small piece of twig is used, but in budding only a single bud (or " eye ") is used, which in both cases forms the rudimentary material for the new tree. This obtains its root from another plant, whereas the remaining part develops vegetatively from the desired plant. In horticulture we are familiar with grafting as the method commonly used for fruit-trees, whereas roses are budded.

Cuttings are clipped-off branches, pieces of roots or small shoots, which are induced to strike root directly. Ligneous cuttings (" hardwood cuttings ") are generally familiar from the cultivation of poplars, in which the cutting is removed as a piece of a branch while the tree is in a state of rest. In other cases only the last year's shoots are taken and they are used more or less like herbaceous cuttings (" softwood cuttings "). Lastly one can also use pieces of root or the shoot growing vegetatively from it.

At first sight it may seem most convenient to take up first and foremost propagation by using cuttings in one form or another, because in this way is ensured the vegetative reproduction of the whole of the plant. By this method the material is identical both in the root and in the upper parts. In its favour, too, are the examples, well known in the breeding of fruit-trees, of a very considerable effect upon the development (growth-form) of the grafted twig through the use of different roots (stocks). It must be remembered, however, that in horticulture a very great deal of research work has been done just in order to discover stocks with these qualities. If grafting is done only on seedlings of the same species, and only well-developed uniform progeny are used as stocks, it is surprising how uniform the lots are that are obtained.

When speaking of the effect of the root (stock) it must be kept clearly in mind that it is only a question of a modification, a vegetative evolution of the scion, not of any genetical change. No changes in the inherent tendencies of any plant have been proved as a result of its growing on a foreign root.

Grafting is an easy and reliable method, which may be used in practically all cases. It is the method which has most often to be used, and it has so many different forms that it must be dealt with first and most intensively. It is especially important that the forest-tree breeder should master this technique, so that he can adapt it for his special conditions and requirements.

Common to all grafting is the fact that a piece of a branch (the scion) is transferred from the desired tree to another plant (the stock), from which, at the same time or later on, the original top is removed. It is thus the transferred twig which alone comes to form the new plant on the foreign root. There is a division of the selected examples into several others, in which the inherent characteristics are preserved unaltered in all parts of the plant above the point of grafting.

The most important essential in order to obtain successful graftings is to have healthy stocks of good growth. They are most often young plants from two to four years old. In addition, one must search for vigorous, well-ripened and fresh scions of shoots of one or several years' growth with well-developed buds.

Slender soft water-shoots or short, thick-jointed top branches are not so easy to work with but in the first graftings from a selected tree there is often no other choice. The work in that case must then be done with special care. As soon as fusion has taken place, the originally weak twig will quickly produce good scions for subsequent reproduction.

Whether one has to use one-year-old material or material several years old will depend upon the tree-species and on the grafting method one wants to use. If one-year-old twigs are used, it will be an advantage to cut away the topmost part of the twig, which is often not so well ripened.

Some discrepancy in development between scion and stock is most often an essential for a satisfactory result; the stock should as a rule be in growth, while the scion is still dormant. When the opposite is the case, the grafting does not succeed. The scions are therefore usually cut in late winter, while the buds are still in a state of complete rest. The twigs are stored, without being cut up into the ultimate lengths, in small bundles on a cool, not too moist, spot with their lowest parts heeled into gravel and otherwise covered with peat litter, spruce brushwood or other material to isolate them against desiccation and changes of temperature. It is necessary to keep them as fresh as possible, and at the same time backward in development. In grafting the inosculation should take place so rapidly that it occurs prior to the unfolding of the buds of the scion.

A good grafting-knife is very important; a knife specially manufactured for the purpose is obtainable in the shops. It is a strong knife with a thin, straight blade and single-edged and is ground only from one side and can thus more exactly adapt itself to a flat cutting surface. It is made of par-

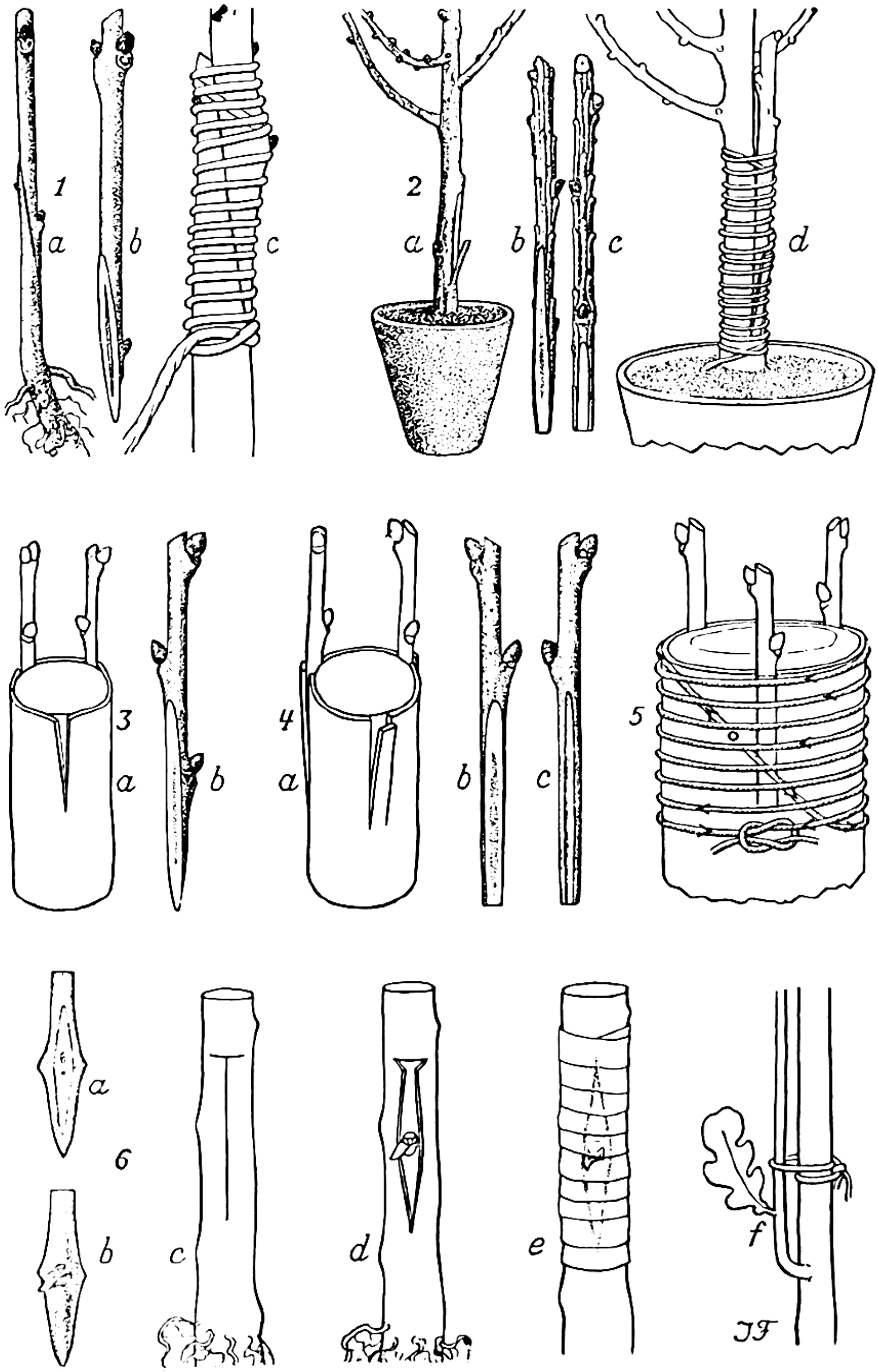

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FIG. 13. GRAFTING AND BUDDING.

1. Whip-grafting. (a) Scion and stock placed together so that the two cut surfaces cover one another. (b) Trimmed scion. Note the bud opposite the basal scion cut and the lop just above a bud. (c) Binding. Begun from above so that the first coil takes in the topmost edge of the stock and the last one lies below the lowest edge of the scion. The binding is fastened by bringing the string back under the last coil.

2. Side-grafting. (a) Potted stock with incision. (b and c) Trimmed scion. (b) Inner face and (c) Outer face. (d) Binding, carried out as described for Fig. 1c.

3. Bark-grafting on old stem. (a) On both sides of the vertical cut the bark is loosened so that the scion can be slipped into place. (b) The trimmed scion.

4. Veneer-grafting. (a) The bark-flap lying between the two vertical cuts is loosened. (b and c) The trimmed scion. (b) Inner face and (c) Outer face.

5. Binding on old stem. With the little finger and ring-finger of the left hand the string is pinched against the palm of the hand and held at (o) with a suitable loose end down along the stem. With the other three digits the scions are supported and care is taken to hold the bark-flaps in place. With the right hand the binding is then carried out, so that the topmost coil lies just below the bark edge of the stock and proceeds in tight, even coils to just below the vertical slit in the bark. The loose end is then carried in one turn round the stem in the opposite direction and the two ends are knotted. (The sketch is simplified. The coils should lie closer together.)

6. Budding. (a) "The eye" seen from the interior. The sapwood not removed. The vascular bundles seen as two spots. (b) "The eye" seen from the exterior. (c) The **T**-shaped incision in the stock. (d) The bark loosened, and the eye slipped into place. (e) Binding with adhesive tape, raffia or rubber band. In budding always commence the binding from below and there should be at least four coils: 1. At the start of the vertical incision. 2. Just below the leaf-stalk. 3. Just above the eye and 4. should cover over the transverse incision. In the last coil fasten as in whip-grafting. (When sealing with adhesive tape the coils follow closely one after the other, and the eye is completely shut in.) (f) The following spring, the shoot bound up to the stump which is later removed.

ticularly good steel, so that it can cut keenly and keep its edge in spite of operating in the often hard wood. It is sharpened first on a fine carborundum stone, next polished on a piece of slate, and finally stropped on a leather strap adapted for that purpose.

It should be handled quickly, accurately, and cleanly. The cuts should be made with a steady hand and should present completely flat surfaces. The surfaces of the wounds should fit against one another in the best possible manner, and they must not be dirty or become wet. The binding is done with a tight-fitting but not too tight piece of tape.

The grafting is most often carried out either just before or at the commencement of the growing period in the spring, but it can be performed at any time when the bark can be easily loosened. In this country a good time for the grafting of several important conifers recurs in August. When grafting wax is used, it must be kept plastic enough without being too hot. Its application must be done carefully, so that no crevices are left through which desiccation may arise.

In grafting, various forms of incision may be employed. Distinctions are observed between whip-grafting, side-grafting, bark-grafting, and veneer-grafting. These are shown in Fig. 13, 1–5, and an explanation is given in the accompanying text.

In addition triangulation should be mentioned. It is rather difficult, but if it is correctly performed it provides a satisfactory and secure inosculation. The scion in this method is cut along two surfaces, which start from the same height, have the same length, and lie at right angles to one another. The stock is cut through with a horizontal cut, and running down from the cut surface a wedge-shaped incision is made, which corresponds to the cut surfaces of the scion. The scion is put in place and tightly bound into the incision.

Whether one should use one form or another for the incision must be left to practical opinion, arrived at on the basis of personal skill and training. Some have great difficulty in learning the knack, whereas others are green-fingered to such a degree that almost every graft succeeds.

With regard to the size and treatment of the stock there are various ways of proceeding. Grafting in *greenhouses* will certainly appear to be rather odd to most foresters, and I myself from the earliest years have stressed that it should be restricted as much as possible. In this country we are now able to work to an overwhelming extent with grafting directly in the *open*. It is, moreover, important to be able to graft on *rather old trees*, as this may bring special advantages. Nevertheless we cannot entirely escape from grafting in greenhouses for, among other things, it has the advantage that the work can be spread over a time of the year when it is impossible to operate in the open.

The stocks for use in the greenhouse must be planted in flower-pots in the spring before they are used. They should be in a satisfactory state of growth when the grafting has to be done. During the winter they are kept in the flower-pots on a bed in the nursery or in a frame, where they can be protected against the worst frost. With us they are taken inside in February–March in order to bring them on by cautious heating. As the grafting must be done when the leaves flush, which occurs rather sooner than in the open, in this case the scions can be taken directly from the forest and storage is thus obviated.

For grafting in greenhouses side-grafting is extensively employed. It is used with satisfactory results for *Pinus* (pine), *Picea* (spruce), *Abies* (silver fir), *Larix* (larch), *Pseudotsuga* (Douglas fir), *Quercus* (oak), *Fagus* (beech), *Alnus* (alder), and *Betula* (birch). When we do not make use of grafting wax, the plants are so deeply embedded in moist peat litter that the point of grafting is completely covered. It is a great advantage to be able to make use of a propagating frame, in which the plants can be protected for some time against too strong evaporation. They are bound with cotton thread, as bast will rot too quickly. After inosculation the band is carefully removed, and the plants are gradually hardened off for planting out in the open.

For grafting in the open in the nursery the first essential here is again to have young, vigorous plants for stocks and these have to be grown on the spot at least a year before the grafting is performed. As examples of what is required the following ages may be mentioned: *Larix* (larch) and *Fraxinus* (ash) as 1/1 transplants, *Pseudotsuga* (Douglas fir), *Pinus* (pine), and *Fagus* (beech) as 2/1 transplants, and *Picea* (spruce) as 2/2 transplants. This means that the plants have been put into the nursery at one or two years of age respectively and have waited for the grafting for one or two years. After the grafting they must remain standing for yet one more growing season.

It cannot be denied that by this method the plants make large roots, and that the grafted plants have a rather difficult time when transplanted in the year after the grafting. There may thus be some advantage in planting the stocks out on the place where they are to remain in the forest and in making the grafts there.

For grafting, mild calm weather is best, and there must be no grafting during frost or rain. Besides side-grafting, most use is made of whip-grafting and bark-grafting. They are sealed with wax.

When grafting in the open by these methods we have had good results with pine, larch, Douglas fir, ash, beech, oak, elm, and alder. We used this practice for the first time in 1941 and have since developed it considerably. It will certainly come much into use in forest-tree breeding, as it not only enables us to do without the expensive greenhouse, but seems to give quite satisfactory results.

Larch is one of the easiest trees to work with. In 1949 we grafted one lot on to 1940 stocks, and it had 67 per cent. success. See Fig. 58. With beech, which has hitherto been one of the most troublesome; in 1952, after grafting on 2435 stocks, a count in the autumn showed that we had obtained a 71 per cent. success.

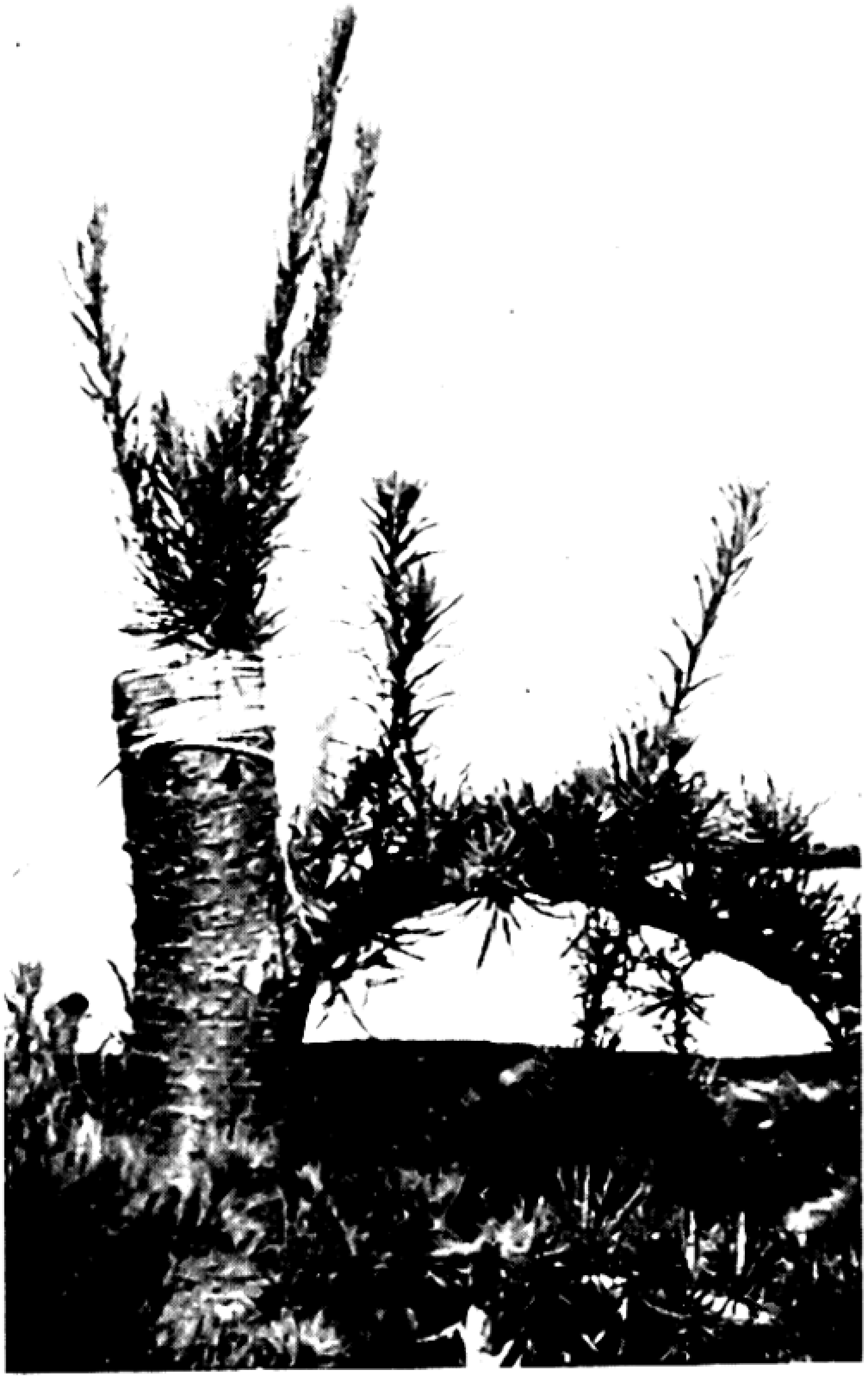

Fig. 14. Hybrid larch, S.126^3. Grafted in the open on 6th August 1941. *Photo*, 3rd July 1942.

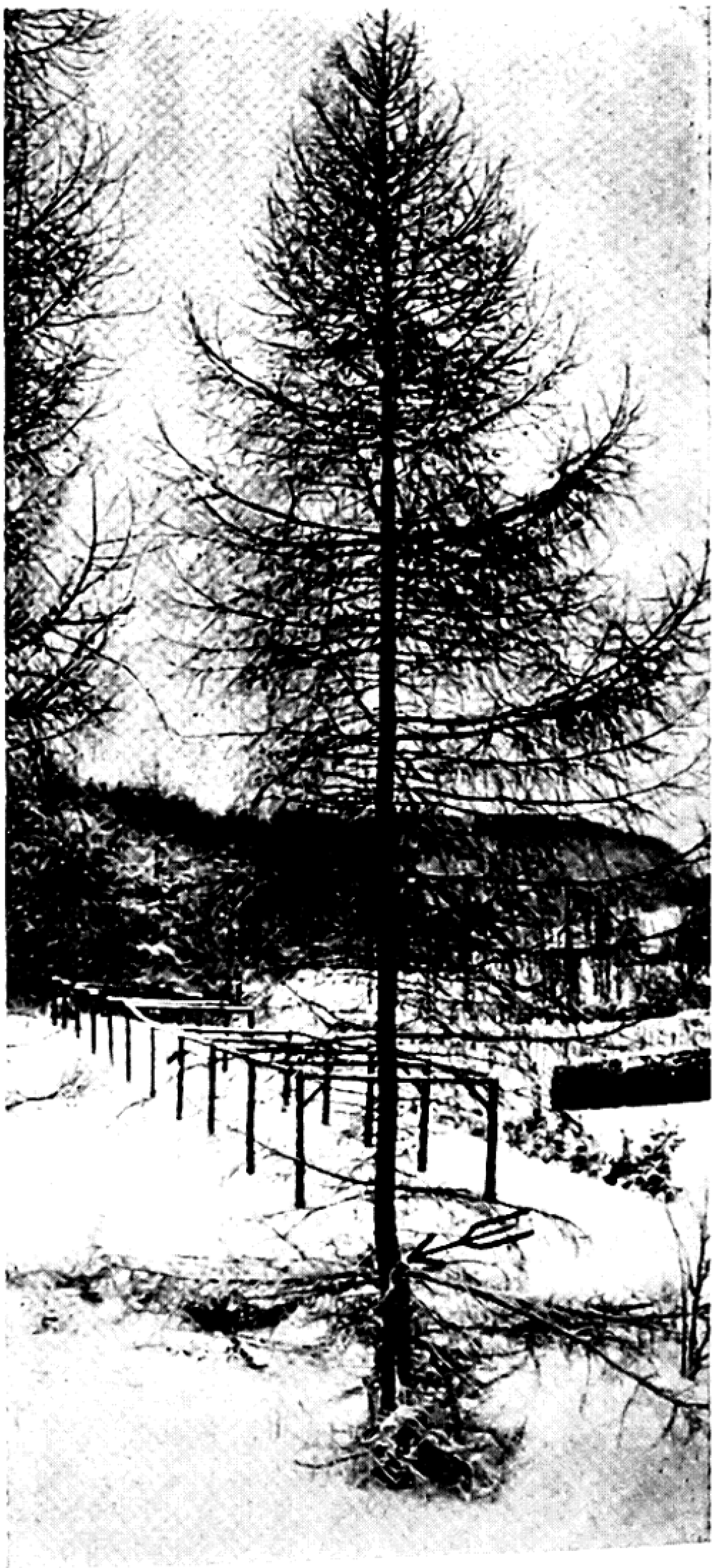

Fig. 15. The same grafting as in Fig. 14. *Photo*, 10th February 1954. The arrow indicates the point of grafting.

In " root-grafting " (" hand-working ") the work is done with loose, uprooted stocks. These are dug up in the autumn, heeled in on a sheltered spot, from which they can be brought in for grafting, although the weather has otherwise put a stop to outdoor operations. Late in winter and in early spring the plants can be taken out of the trench and kept in the house during grafting.

Unfortunately we have so far been able to use this method on a large scale only with ash. The method used was whip-grafting.

After grafting, the plants are put out once more in the trench and transplanted like other transplants in the spring-time. This is a cheap and rapid method. One grafter with an assistant for applying the grafting wax and carrying the plants has here made about sixty graftings in an hour.

After the fashion of the " top-working " of old fruit-trees by the gardener, it may sometimes be an advantage to graft on to large transplants or trees. The purpose of this may be to get a rapid production of scions, or one can maintain a flowering which has already started. Satisfactory work can be done with stocks of 5–10 cm. in diameter at the point of grafting, which it is convenient to fix at breast-height. After carefully cutting off the topmost part of the tree the cut surface is then smoothed with a strong knife. The cut is made obliquely in towards the centre, so that the bark remains quite smooth, and it is best to use veneer-grafting. In 1942 we were able to give a report of the first successful graftings by this method with ash, aspen, oak, and larch (*Dansk Skovforenings Tidsskr.*, 1942). From this Fig. 14 is reproduced, which may be compared with the same 13-year-old graft (Fig. 15). In 1942 and 1943 it was extended to pine, spruce, Douglas fir, beech, and alder, with excellent results. It has the advantage that the scion develops vigorously upon the severely cut-back stock. A year or two after the grafting it is thus possible to harvest some of the material for further graftings. This can be expanded into the use of proper " multiplication-gardens ", which will certainly be of importance for large undertakings or can be used as a provisional measure.

As an example, reference may be made to one instance with larch. In the spring of 1946, 118 larches, which were about 3 cm. in thickness at the point of grafting, were grafted with a total of four hundred scions. Without ruining them for further production of twigs, when grafting was done two years later twelve hundred and fifty scions were cut from them. Vigorous vegetative development occurs as a result of the disproportion between the small pieces of branches used and the much more vigorous stock.

By a more moderate cutting-back of the individual branches and subsequent grafting in the crown of older, fruit-bearing trees, it is possible to get a different result. By that method one can successfully use scions capable of flowering and preserve such a balance between stock-tree and scion, that the latter continues to flower in the same manner as the parent tree.

It is a constant object of experiment to get scions from young plants in order, after such a form of grafting, to bring about earlier flowering than normal. Reports of experiments with fruit-trees may give some grounds for optimism. Simply to be able to perpetuate fruit-bearing which has occurred upon an older tree by grafting on to an appropriate rootstock-tree, may present a considerable advantage (p. 90 and Fig. 24).

It is important to see that the bindings of graftings are loosened before they become too tight. If it should be necessary, a new binding must be applied so as to assist the union for some time longer. The scions are often attacked by insects, and these must be dealt with by powdering or spraying. This occurs only in the first year, however, when the shoot development is abnormally late.

In the case of graftings on young plants, when it is the object to give the plant a normal appearance, only one strong shoot is kept, which, if necessary, is guided in the proper direction by being tied back so as to grow vertically. On older stems, when the object is to get an abundance of vegetative material, it is a good thing to do some thinning out or heading back of too luxuriant shoots. This applies only in the first year, when there may be a danger of them snapping off at the point of grafting because of the unnaturally strong growth.

Inoculation (bud-grafting, budding) is a form of grafting in which use is made of a single bud (" eye ") only. It gives a better utilization of the material, and the operation can be carried out more quickly. It causes a smaller wound and gives a better union. It is therefore a good method for those species which permit of reproduction in that way. Amongst our Danish forest trees it is so far of practical importance only for ash. Experiments with oak have given good plants but it has not yet been possible to do it on a large scale. Amongst tropical tree-species it is commonly employed for *Hevea* (the rubber tree).

For inoculating, just as with grafting proper, one must have healthy stocks in good growth. For ash the

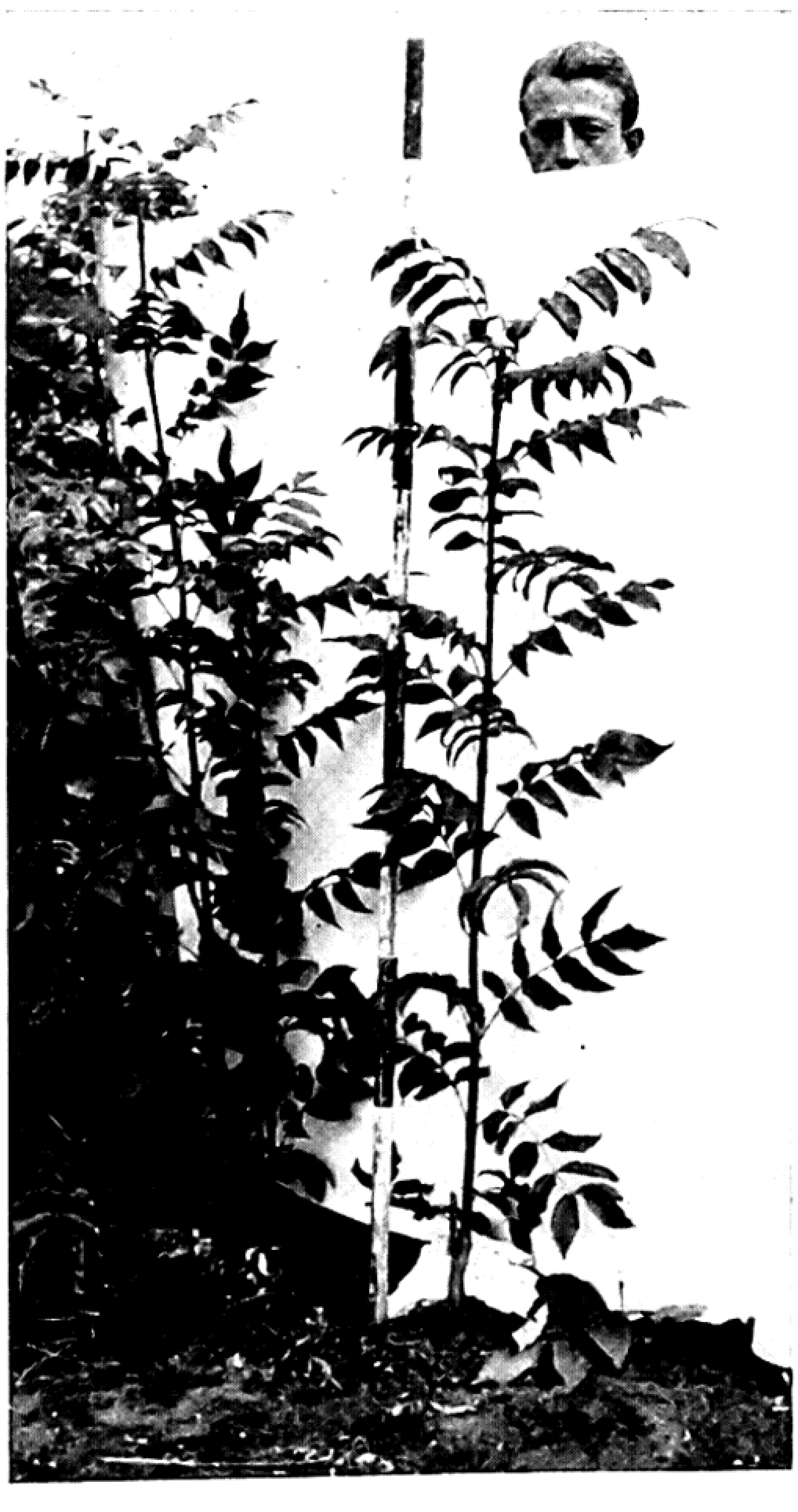

Fig. 16. *Fraxinus excelsior* L. Budded 15th August 1943; *photo*, 13th September 1944. Height 130 cm. (5·2 ins.). *n.b.* The stump from the original plant is cut away on transplanting.

thickness at the root-collar should be from $\frac{3}{4}$ to 2 cm. (0·3–0·8 in.). The twigs from which the " eyes " are to be cut must be well ripened and have sound, well-developed buds.

Only the intermediate buds on each twig are suitable, and the twigs must be cut immediately prior to the inoculation. The leaves and stipules are cut away but a piece of the leaf-stalk is retained as a support during the operation. The twigs are kept well protected right up to the removal of the " eyes ". The budding knife has a thin blade of good steel. It has on the back a bark-lifter, or the handle of the knife can be shaped for that purpose. Details of the operation are shown in Fig. 13 (6).

For ash the budding is done in the height of summer, in July–August. In the following spring the stock is cut back so that only the inosculated " eye " is likely to burst. In the autumn the plant is ready for transplanting. (See Fig. 16.)

In contrast to all forms of grafting the other group of methods of vegetative reproduction by *cuttings* has the advantage that the products stand on their own root, so that the propagation is concerned with the plant as a whole.

Hardwood cuttings are known in the case of poplars and willows. They are cut from the ripe wood late in the autumn or early in the winter, before they have experienced too much frost. Substantial, well-developed shoots must be selected. They are usually 20–25 cm. (8–10 ins.) long, and such that the top is a short distance above the topmost bud, while the bottom is cut off just below a bud. They are over-wintered in a sheuch and lined out in the nursery the following spring. It is a very easy method of reproduction, which in forestry, however, is of small importance for species other than poplars and willows.

Although other forms of cuttings demand special procedures, they attract a great deal of attention, as they provide us with the opportunity of propagating a number of species. Although these require bell-glasses, perhaps heated frames, or even greenhouses, that must not be allowed to deter us. Once one has worked up the technique for the propagation of tree-species by cuttings, it can offer great advantages. The principal one is that plants are obtained in that way which are identical in respect of both root and top, and in addition it can be a comparatively cheap method of procedure, even when, to begin with, it may seem rather complicated.

The best prospects for root formation occur with young shoots, not yet one year old, which are often taken when they are not quite ripened off. Herbaceous shoots of that kind require, however, to be specially protected in order to be kept alive until after the completion of root-formation. Here it is that we must find the correct technique. Horticulture has carried out good work by using it for the so-called garden forms of peculiar growth, colour or appearance. They generally seem to be easier to propagate than the " true species "—and the easiest has presumably also been to some extent preferred. There is a great deal to show that there is a similar individual variation amongst trees valuable to forestry, and that in its way it may be a help to us.

Here in Denmark the work must be relatively expensive, because of the

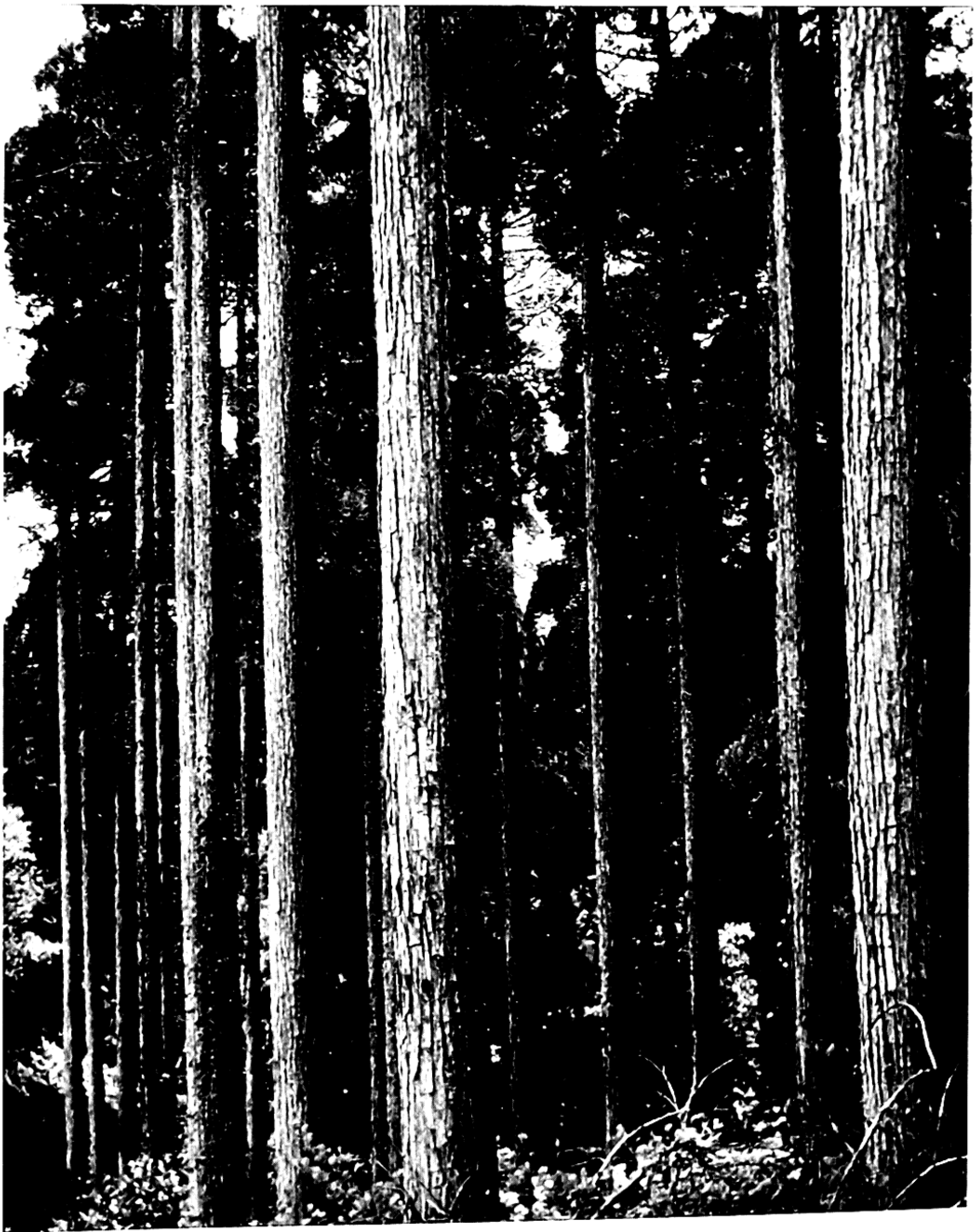

Fig. 17a. *Cryptomeria japonica* D. Don. Clone " Higo-measa ". 165 years old. Umaisi National Forest, Kumamoto, Japan. *Photo:* M. Kirihara.

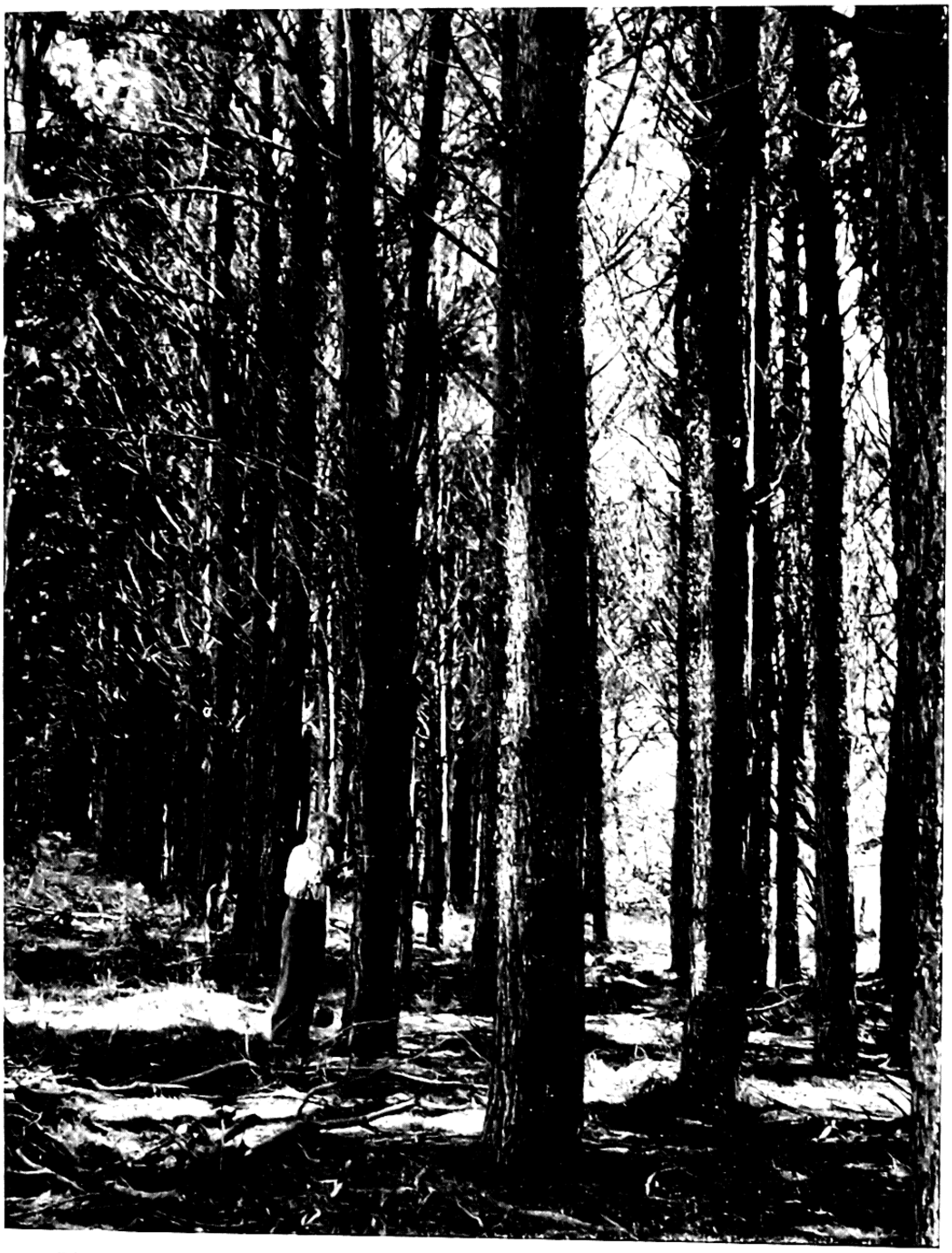

Fig. 17b. *Pinus radiata* D. Don. Monterey pine. Cuttings planted in 1930. Palmerston North, New Zealand. New Zealand Forest Service Photo, 1954.

unsuitability of the climate. Other countries are more favourably endowed with milder and less windy weather.

As examples of the successful use of cuttings reference may be made to Fig. 17a and b. Mr. Ryookiti Toda during a course of study at the

Arboretum presented me with a beautiful example of the use of cuttings which has been well-known for many years in Japan. It refers specifically to *Cryptomeria japonica*, of which there are indeed several named clones.

With similar kindness I have obtained from the New Zealand Forest Service the illustration reproduced in Fig. 17b. This shows the use of cuttings in a similar fortunate climate with a favourable tree-species (*Pinus radiata*), which has been at a lucky age, one- to two-year-old plants.

The plants for this stand were raised from cuttings, which were lined out as small broken-off twigs in a nursery bed, and it was really done only in order to increase the number of plants. These were not cuttings from a single plant, so that the stand does not have the uniform look which would otherwise have been obtained. It shows, on the other hand, how easy propagation has been in this case, and how cuttings can develop into trees in full growth.

FIELDING from Australia has furnished a report of valuable experiments with cuttings from a long list of different individuals of *Pinus radiata* (see p. 212). When one becomes acquainted with the great individual variation in this tree-species it does not need much imagination to realize the value of an additional cheapening of the technique of vegetative reproduction. What is already being done offers great advantages for the expanded production of seed on the basis of an intensive analysis of single individuals.

Here with us it seems at the moment that it should be of most importance for *Picea Abies* (Norway spruce) and *Thuja plicata* (Western red cedar), although success has also been achieved in getting cuttings of several other forest trees to strike root. As regards the method of procedure the following points may be mentioned.

When the shoots are suitably ripened off, rather large branches are cut off, which are at once protected against desiccation. The young shoots must not at any time become lax and drooping, so they are therefore put into water as soon as possible. When they are thoroughly saturated from taking up water, the desired shoots are torn off with a suitable " heel ", which can later be smoothed with a knife. They are again kept in water or growth-substance until they are dibbled in, for which they must not be kept waiting too long.

In a frame, such as is commonly used for pricking out in gardening, a suitable bed is prepared in advance. On top this consists of a layer of pure gravel or sand about 5 cm. (2 ins.) thick, beneath which is a layer of light mould mixed with gravel. The aim of this is to get the roots springing from the lowest part of the cuttings to spread themselves in a light but at the same time sufficiently fertile material, whereas the upper part of the cutting is rather kept in place by the pure gravel, which, moreover, also shields it against desiccation.

Before being dibbled out the herbaceous cuttings may be treated with a growth-substance. These are usually preparations with indolyl acetic acid or indolyl butyric acid. They may be in liquid solution or powder form, but in this connection reference must be made to the special literature on this subject. The growth-substance can have a good effect, but it must not be forgotten that, in spite of everything, what counts most is to strike the right time and look after the cuttings carefully. There is no disparagement in saying that the growth-substances are not a charm, which can enable us to forget the other factors. (See, for example, C. MUHLE LARSEN: "Experiments with Soft-wood Cuttings of Forest Trees", *Det Forstlige Forsøgsvaesen i Danmark*, 1946.)

Where drying wind may have a harmful effect, immediately after the dibbling in they should have a covering of glass, which is not replaced with light shading until later.

There are many ways of growing cuttings from young material. Good results may be obtained with very young cuttings in the summer time, when they are taken just after the lengthening of the shoot. In other cases this does best with cuttings made in the late autumn or early spring. If there is a possibility of working with a greenhouse or an electrically heated frame, that will be a great help.

Just as with grafting, the results depend upon the interplay between the tree-species, the climate, and other locality factors. It is thus impossible to lay down definite rules. Sound opinion favours the view that pioneering experiments must be carried out before making use of existing experience in the best way possible later on.

As examples it may be mentioned that Norway spruce cuttings, when dibbled in in 1951, and without the use of growth-substances, have given about 70 per cent. of plants. *Thuja* was dibbled in in 1951 and again without growth-substances produced 80 per cent. of plants.

For trees with the ability to form root-shoots, vegetative propagation can be extended to include reproduction by root-cuttings. The simplest form of this method is to cut off the pieces of root as is done with woody cuttings. They are dug up in late autumn or winter, cut up and put into bundles, so that they lie with their "top-ends" all in the same direction. They are heeled in and completely covered with soil before being set out in the spring like woody cuttings. They should be set so deeply in the soil, that the ends which were nearest the tree are just flush with the surface. Of the shoots which spring up only the strongest are kept, whereas the root ought to spread itself as much as possible. It is an advantage to have a light but at the same time sufficiently moist soil.

When taking up the young plants one can often, without damaging them, cut off a good many one-year-old pieces of root from each individual plant and so obtain material for quite a rapid increase in numbers. For poplars this procedure is applicable in practice with *P. tremula, tremuloides, alba, canescens,* and *grandidentata,* and amongst other tree-species special attention should be drawn to robinia.

A much more rapid reproduction by means of root-shoots can be reached by using the so-called R.S.-cuttings. The method was devised at the Arboretum here by MUHLE LARSEN (C. MUHLE LARSEN, loc. cit.).

For R.S.-cuttings use is made of the young, herbaceous shoots which come up on cut-off pieces of root, after they have been allowed to sprout. If the dug-up pieces of root, planted out in a box with peat litter, are placed so that air and warmth are controlled, there normally springs from each separate piece of root quite a number of small shoots, which push out towards the surface. MUHLE LARSEN has shown that these shoots, when 2–4 cm. (0·8–1·6 ins.) in size, and just after they have formed their first green part, are very ready to strike root of themselves.

By pulling them off as they arise and pricking them out, they are speedily able to develop a fine root-system, and one can reap a considerable harvest. One great advantage of this procedure, too, is that one gets a healthy root, which is freed directly from the larger portion of root of the old tree. The method demands care, however, and accurate working in order to avoid rot and other difficulties while working in greenhouses. Taking this into account, the method can give excellent results and will probably be extended to other tree-species which have a natural capacity to form root-shoots. With us it has been mainly used for poplars which form suckers.

The review which has been given of the various forms of vegetative reproduction is, I hope, sufficient to show that we have great opportunity to provide ourselves with numbers of genetically identical individuals from certain desirable trees. A collection of individuals originating by division by one or other form of vegetative reproduction from a single individual, is called a *clone.*

By a not prodigious amount of work we can furnish ourselves with clones of desirable outstanding trees. Some of the most important uses of these will be mentioned in the sequel, since they seem to me to be the most important basis for forest-tree breeding in its modern form.

CHAPTER VI

SEED-GARDENS

THIS is our "trump card" in forest-tree breeding. It is the means for the growing of seed through controlled pollination in any desired quantity. As described in the following paragraphs, I gave prominence to it in 1934, and ever since have steadily become more convinced that I was right. Further consideration of the matter may be introduced with an example.

From two selected young larches scions were cut off in the spring of 1939 to furnish two clones, V.419 and V.420. Grafting was carried out on two- to three-year-old stocks, and two years later these were planted out in the Arboretum. They have since been steadily thinned out so heavily that those which remain can grow up into trees with freely developed crowns and with branches right down to the ground.

Both clones have borne seed abundantly, and the yield measured in cones has been:

For the 1948 *flowering:* the tenth year in the age of the grafts.
V.419 gave 2340 cones as the average for 4 trees.
V.420 ,, 1267 ,, ,, ,, ,, ,, 6 ,,

For the 1952 *flowering:* the fourteenth year in the age of the grafts.
V.419 gave 5570 cones as the average for 2 trees (height 10·70 m. (35 ft.)).
V.420 ,, 3600 ,, ,, ,, ,, ,, 2 ,, (,, 10·26 m. (33·7 ft.)).

A scion from the first vegetative propagation (V.419) has thus grown into a tree which, in its fourteenth year, was standing with a crop of 5570 cones, whereas that in the second case (V.420) produced 3600 cones.

For the two clones the yield of seeds in the fourteenth year after grafting was as an average for two trees in each case:

V.419: 1160 gm., or about 220,000 seeds per tree.
V.420: 810 gm., ,, ,, 160,000 ,, ,, ,,

This illustrates to some extent the idea behind seed-gardens. Although both clones bear seed abundantly, it has to be emphasized that they were not chosen because of that attribute. The scions were cut in 1939 from the two plants most promising in form and growth in a group of one hundred plants, which had been planted out in 1937. The group represented a cross between Japanese and European larches, which was made in the spring of 1933 by controlled pollination of a selected Japanese larch with pollen from the largest and finest European larch occurring in this country. Out of the original one hundred plants of the group in question, after various thinnings, there remain thirty-five trees, in which the trees which were the starting-point of the two clones mentioned are not distinguishable by any abnormally abundant fruiting. The stand as a whole gives a satisfactory seed-yield. From the seed-setting in the fifteenth year (1948), which was as good a cone year as 1952, it may be mentioned that six trees bore on the average 2360 cones. It varied from 692 to 4400 per tree.

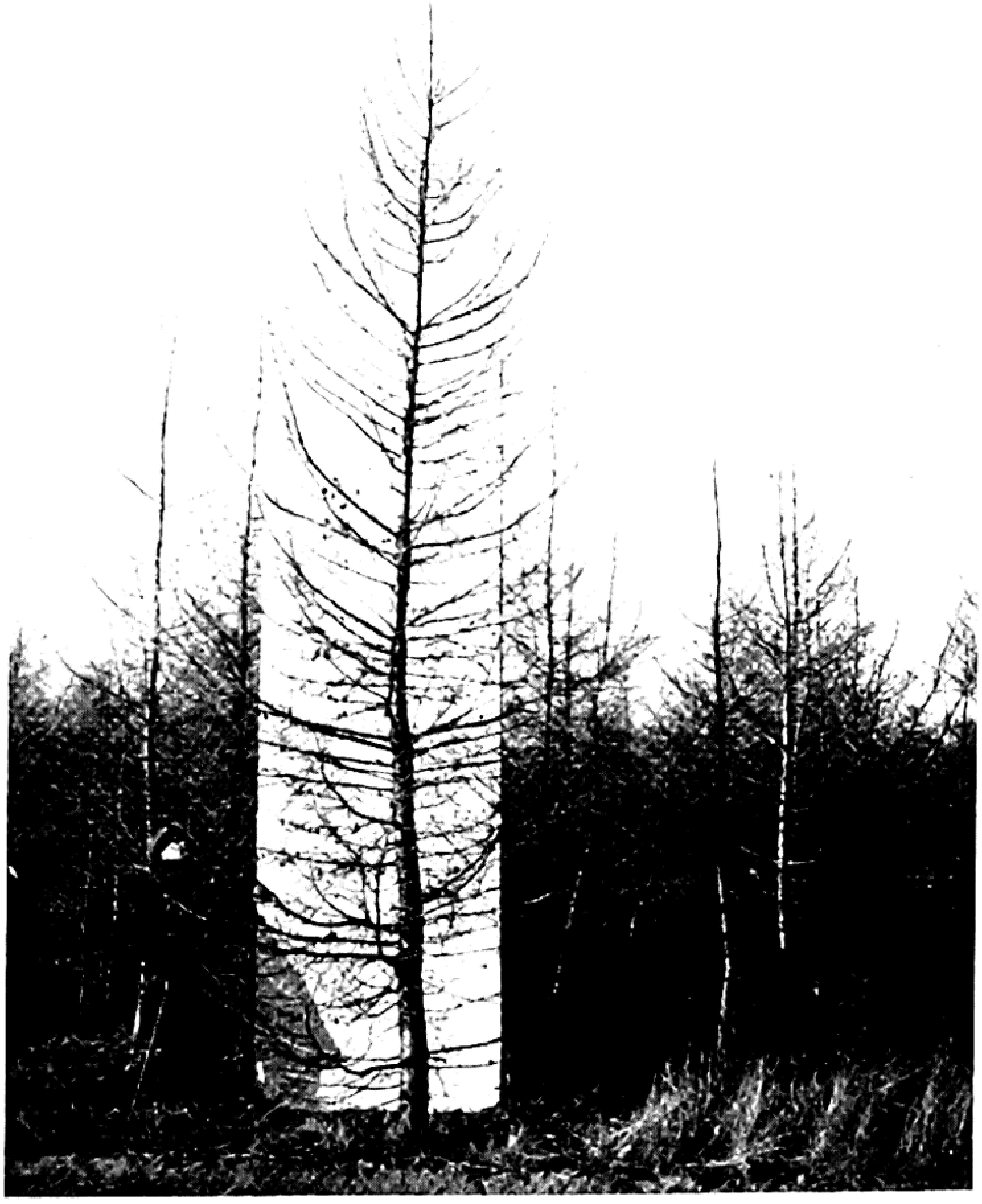

Fig. 18. *Larix*. Hybrid larch; clone V.419. Grafted 17th March 1939. *Photo*, 4th January 1947. One out of the four trees, which, after flowering in 1948, gave on the average 2340 cones.

If the two original larches, now nineteen years old, had stood entirely isolated in the same manner as the five-year-old grafts, then they would certainly have given more cones and more seed than the graftings. It will be most usual, however, for the tree which is chosen for seed-production to stand cleaned up in a forest stand, so that it becomes difficult and costly to provide so great a yield that it can compete with the yield on a comparatively young graft from the same tree, when it has been possible to give the graft the correct isolated position.

There is a much greater advantage, however, in that instead of taking one graft we can produce them in any desired number. When we began the grafting of the clones V.419 and V.420 from the five-year-old seedlings, fifty scions were cut from each plant, without harming the plants. In respect of an example from V.420, reference may be made to Fig. 19, 1, a and b. It shows a five-year-old graft before and after it was pruned and had given material enough for about 575 new grafts.

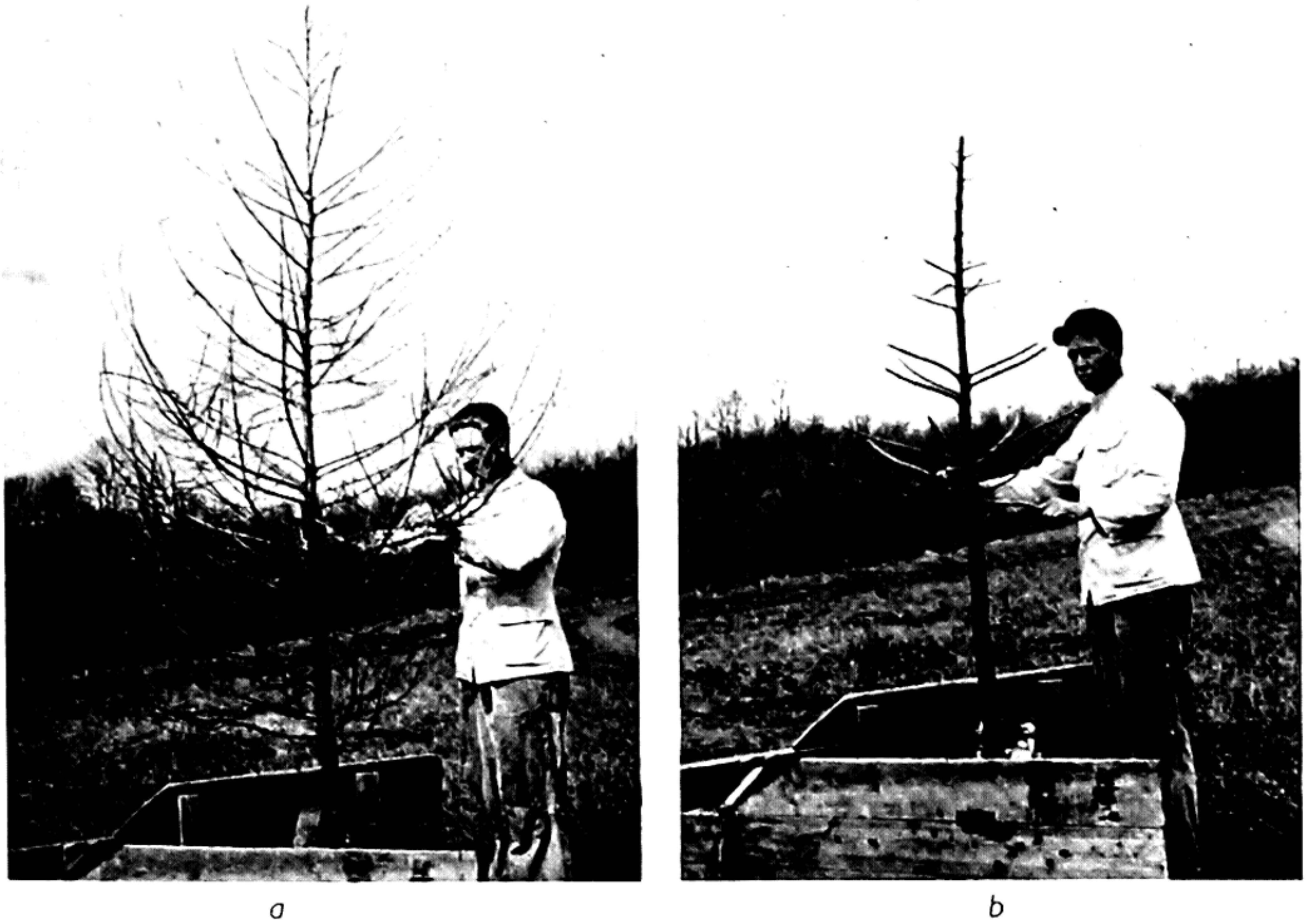

Fig. 19[1]. *Larix*. Hybrid larch; clone V.420. Grafted 17th March 1939. *Photo*, 18th April 1944. (a) Before pruning off the scions. (b) After pruning away of scions for 575 graftings. The plant itself was not damaged to the extent that it could not give in the following year a new harvest of vegetative material.

If we were now to assume that for each of the two clones we had kept the first fifty grafts from 1939 in an entirely isolated position, and had thus been able to harvest from each 1160 and 810 gm. of seed per tree, that would amount in all to about 100 kg. (220 lb.) of seed. On one hectare (acre) at that age there could easily be fifty (twenty) grafts, although one would also have them mixed up with an equal number of other larches for their pollination. In the fourteenth year after grafting that would mean a yield per ha. (ac.) of about 40 (16) kg. for clone V.420 and no less than 58 (23) kg. for V.419. Putting this on the average at 50 (20) kg. of seed per ha. (ac.), and reckoning on about 200,000 seeds per kg., there would be a yield of about 10 million (4 million) seeds per ha. (ac.). With a reasonable germination percentage and ordinary seed-bed preparation, each ha. (ac.) of seed-garden in the fourteenth year after grafting would be able to supply about 900,000 (360,000) plants.

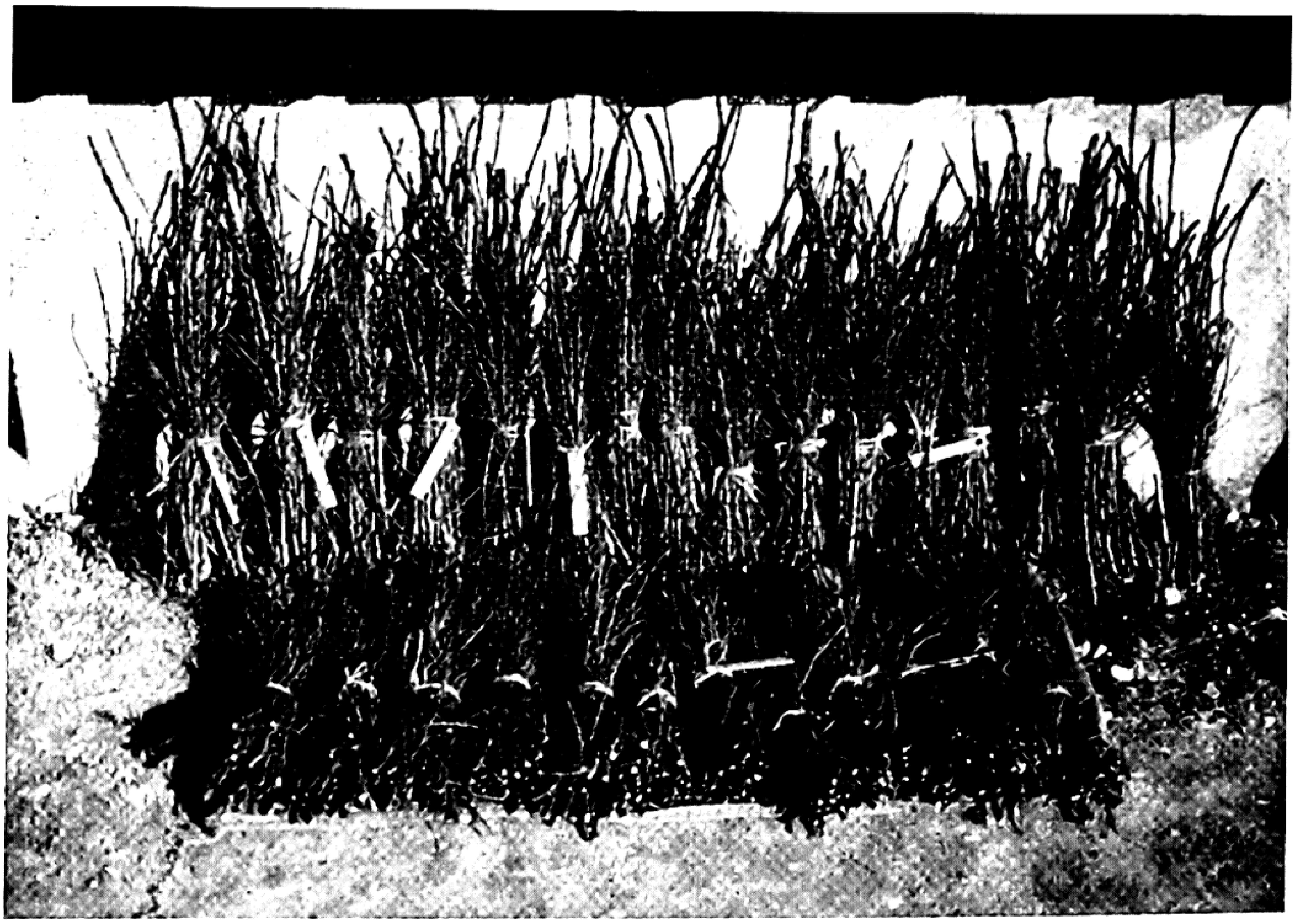

Fig. 19^2. *Larix leptolepis*, Gord. Yield of twigs for cutting up about 2800 scions in one clone (V.975). All were cut from 500 plants grafted one year earlier on to rather old stocks. *Photo*, 10th March 1953.

If we go back in time, the quantities of cones for two trees of V.420 in the years 1945 and 1946 may be given:

V.420: 1st tree . .	253 cones in 1945 and	605 cones in 1946.
2nd ,, . .	319 ,, ,, ,, ,,	252 ,, ,, ,, .
Average . .	286 ,, ,, ,, ,,	428 ,, ,, ,, .
50 trees, 1 ha. . .	14,300 ,, ,, ,, ,,	21,400 ,, ,, ,, .
20 ,, , 1 ac. . .	5720 ,, ,, ,, ,,	8560 ,, ,, ,, .

Converted into seeds, these figures would become about 2 kg. and 3 kg. from 1 ha. (0·8 kg. and 1·2 kg. per ac.) of graftings respectively in the seventh and eighth years after the making of the grafts. This applies to the less productive in seed of the two clones mentioned and when the number of trees is fifty per ha. (twenty per ac.). At that age we might well have two hundred plants per ha. (eighty per ac.) for " seed plants ". With an equal number of pollinators that comes to four hundred plants in all per ha. (one hundred and sixty per ac.), which gives an area of 5 × 5 m. for each plant (16½ × 16½ ft.). In that way we could, in the seventh and eighth years after grafting of clone V.420, have a yield of 8 kg. (3·2 kg.) and 12 kg. (4·8 kg.) of seed respectively. Seed-production is thus linked to the number of grafts and the area, and it becomes independent of the further fate of the original tree.

Other clones of larch, especially of Japanese larch, could furnish still larger amounts of seed and do so still earlier. Larch is one of the most favourable examples, which is followed rather closely, however, by *Pinus sylvestris* (Scots pine) and *Fraxinus excelsior* (European ash), whereas other tree-species will furnish smaller quantities and come later into seed-bearing. Although that is the case, and we have no means of making it equally easy with all the species, there remains an offset that is very important, namely, that we can *increase the amount of seed* with the help of the graftings. A careful cutting-off of the scions affects the tree so slightly that we do not need to expect a reduction of the quantity of seed for that reason. The increase in the numbers grafted rises very quickly, and, assuming the same age and the same treatment, two grafts will give twice as many seeds as one graft, and so we can very rapidly work up to any desired number of grafts and thus gain control over the quantity of seed.

With my great countryman HANS CHRISTIAN ANDERSEN in mind, the story of the " woman and the eggs " may at this point be recalled. It tells how a countrywoman dreamt of the wealth she would obtain if she used a hen's egg for breeding and continued to breed hens steadily. Things did not turn out very well, as she had an accident and had calculated too optimistically.

This should not dishearten us. It certainly costs something to make the grafts, just as it costs something to " set an egg for hatching "; but the " feeding " is cheap, as it can amount only to the expenses of planting and the rent of the necessary area. That represents a considerable advantage and we do not need to harbour any anxiety about our calculations. These are firmly based on experience from our own experiments.

Keeping for the moment to comparisons with poultry-rearing, to-day it is also so carried out that egg-production is kept separate from the production of flesh. Poultry-farms for the production of eggs have become segregated from those concerns the purpose of which is to produce chickens for the table. Not only is it desired to have satisfactory chickens for the table and good egg-layers each by themselves, so that they can be handled in the manner best adapted for the different products, but control over the reproduction is also necessary.

It should be the same thing in forestry. We should keep seed-production and timber-production separate. We should not gather seed in the forest as a by-product, in such a way that we collect the seed only from occasional trees, knowing nothing about the pollination. That is certainly a very common practice, but it nevertheless corresponds to the behaviour of the farmer who, from his motley flock of hens, takes occasional eggs for hatching—and who cannot hold his own in competition with soundly managed breeding-stock. When we do the same thing in forestry, it amounts to precisely the same, even if we ourselves do not observe the results of our improvidence. The loss falls most frequently upon our descendants, but it is none the less unjustifiable on that account.

In respect of the forest it is usual that we only have to consider timber-production, but in doing so it may be well to spare some thought for the seed, which has to replace the forest. When the seed is put into the soil, it possesses certain inherited qualities, which stamp the tree in one way or another. All the good which it can derive from heredity works gratis into the future. The good and poor seed cost just the same in time and attention, until the time we have a merchantable tree. There is no reason to believe that it is the best trees, from the forestry viewpoint, which will win in the mutual struggle for existence; it would be more correct to call them the best fighters.

In addition we must bear in mind that—continuing the comparison with poultry-breeding—we also have valuable " egg-layers ", which by vegetative reproduction we can keep alive as long as we please, and we can multiply them as it happens to suit us. The above example of the two larches, V.419 and V.420, shows this very clearly. Regarded in relation to the long rotation in forestry, the time necessary for the production of quite a large quantity of desirable seed from a single chosen tree is not very long. On the contrary it is very short, and it must be remembered, moreover, that the grafted plants can be placed in any desired locality, where they are isolated from undesirable pollination. In the same way and at the same rate as the seed-trees can be turned out vegetatively, the pollinators can also be brought on. Thus it is possible to achieve the object of *producing seed by controlled pollination in whatever quantities are desired.*

It has already been acknowledged above that larch is easy to work with in this way. In this connection it must be observed, however, that this could not be foreseen at the start of the research. In the years around 1930 we certainly knew that larch is a tree-species which sets seed early. Nothing was available, however, about how easily it could be reproduced in the open by grafting—and it is the combination of the two things which makes the work so easy.

It may, however, be wise to refer to some examples from other tree-species for further illustration.

In respect of *Pinus sylvestris* (Scots pine), one of the oldest and finest trees in Denmark was selected for the first graftings with this species. This tree still stands in " Nødebo Holt " (North Sjaelland) and was produced from a sowing or planting about the year 1772 (*Det Forstl. Forsøgsv.*, Vol. VI, 1922, p. 279). It is one of the oldest specimens arising from the introduction of the species in afforestation work in Denmark, and the seed is thought to have come from Norway. From graftings in 1936 and 1937 we have preserved in the Arboretum a small group of about thirty trees, which are now about 6·5 m. (21½ ft.) high. They were planted in 1941 at 2 × 2 m. (6½ × 6½ft.) apart, which is too close, so that the out-turn from the flowering has not been so large as it might have been. In spite of this the figures give grounds for optimism.

The first thirty-one cones were ripe in the autumn of 1943, when the plants were about 1½ m. (5 ft.) high, and sixty-six cones were available for harvesting in the following autumn. These were enough for the initiation of the first controlled pollinations. In the summer of 1945, 1300 female flowers were counted, and as the area may be put at about $\frac{1}{50}$ of a ha. ($\frac{1}{20}$ of an ac.), there would thus have been in the ninth and tenth years a production of 65,000 (26,000) cones, if we had had one ha. (ac.). Under favourable circumstances this might be enough for about half a million (200,000) plants. In May 1947, 7700 female flowers were counted on the eleven- and twelve-year-old graftings. At a cautious estimate these could certainly have produced 6000 well-developed cones, or about 300,000 (120,000) cones per ha. (ac.). These could furnish about 2½ million (1 million) plants.

Although it has not been possible to repeat the experiment in a more satisfactory manner, what has been said gives some idea of the possibility harvesting offers in a seed-garden of Scots pine. The first application of graftings to Scots pine was intended primarily for artificial pollination, subsequent vegetative reproduction and other operations, so that the results fall short of what the production from the graftings might have been, if they had been handled like a " seed-garden ".

From a fine old *Quercus robur* (common oak), known as the " Østofteeg " (*Det Forstl. Forsøgsv.*, Vol. XII, 1932, p. 100), in the spring of 1938 we made a small lot of thirteen graftings. In their eighth year (1945) they gave in all 176 acorns. As they formed altogether a group of 40 m.^{2} (48 sq. yds.), this may be assessed at about 100 kg. (40 kg.) per ha. (ac.).

In October 1954 the largest tree of the group measured 8·36 m. (27½ ft.) in height and the extension of the crown was 2·5 × 3·0 m. (8 × 10 ft.). The tree had 1375 acorns, which weighed 3·6 kg. (8 lb.). On one hectare (2½ acres) there could easily have been one hundred trees of that size. A seed-garden of one hectare might have given 360 kg. (800 lb.), and as no thinnings should be necessary in later years, a steadily increasing production can be expected.

Of *Fraxinus excelsior* (European ash) one example may be mentioned of three graftings, made in the spring of 1935. The material was taken from a tree which habitually seeded abundantly. Two of the graftings gave 91 gm. (875 seeds) and 128 gm. (1579 seeds) respectively in 1943. In October 1946 all three graftings had seed, and the yield amounted to:

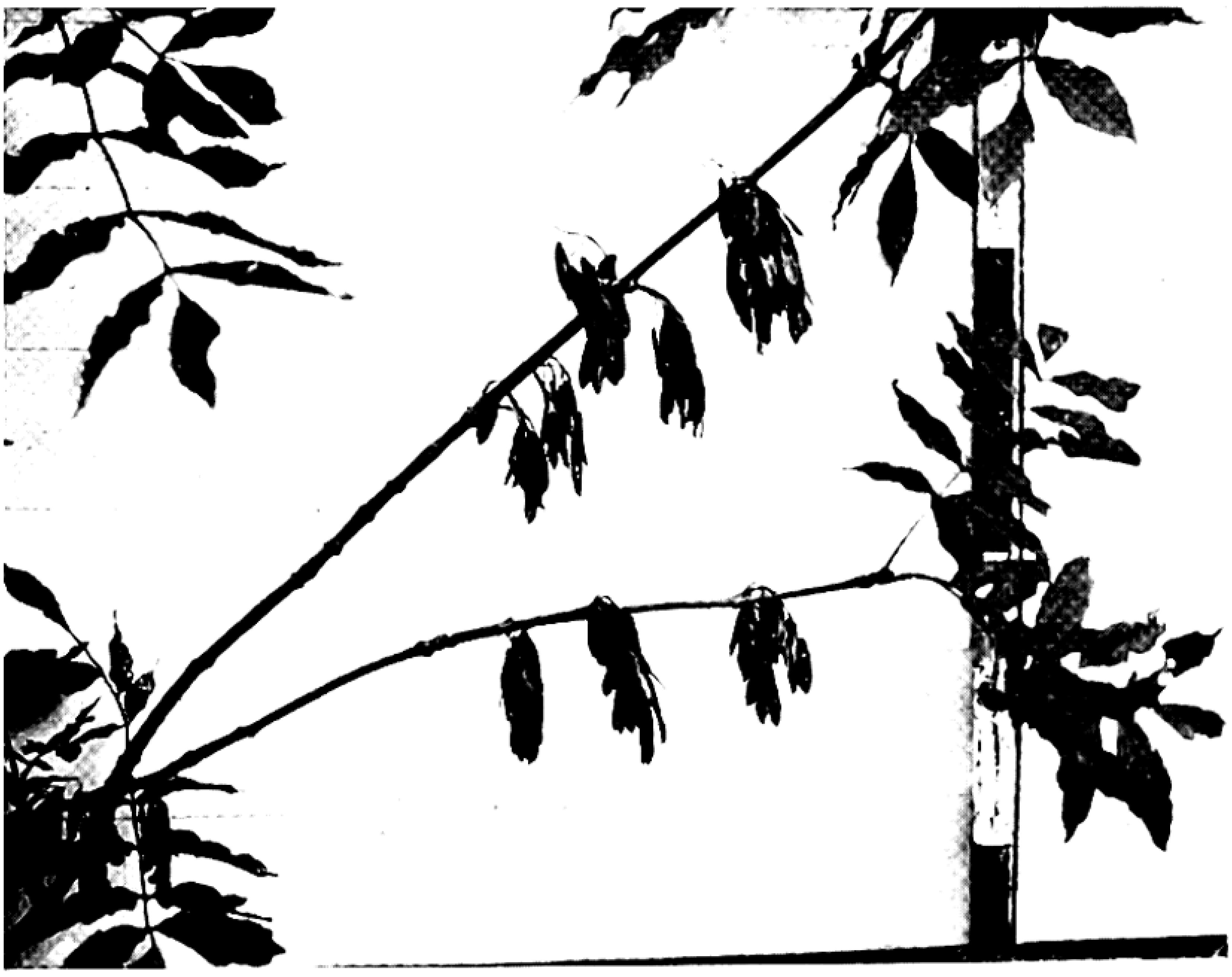

Fig. 20. *Fraxinus excelsior* L. Branch on a graft of bisexual ash (clone V.4), cultivated as a seed-tree. Grafted in the spring of 1935; *photo*, Arboretum, 5th September 1943. The branch photographed has 28 grams of seed or 274 seeds.

2435 gm.—29,300 seeds
2380 „ —26,200 „
1500 „ —15,500 „

6315 „ —71,000 „

This is a good 2 kg. or rather more than 20,000 seeds for each grafting in the twelfth year. Their heights were then 5·4 m. (17·8 ft.), and they stood at a spacing of 2 × 2 m. (6½ × 6½ ft.).

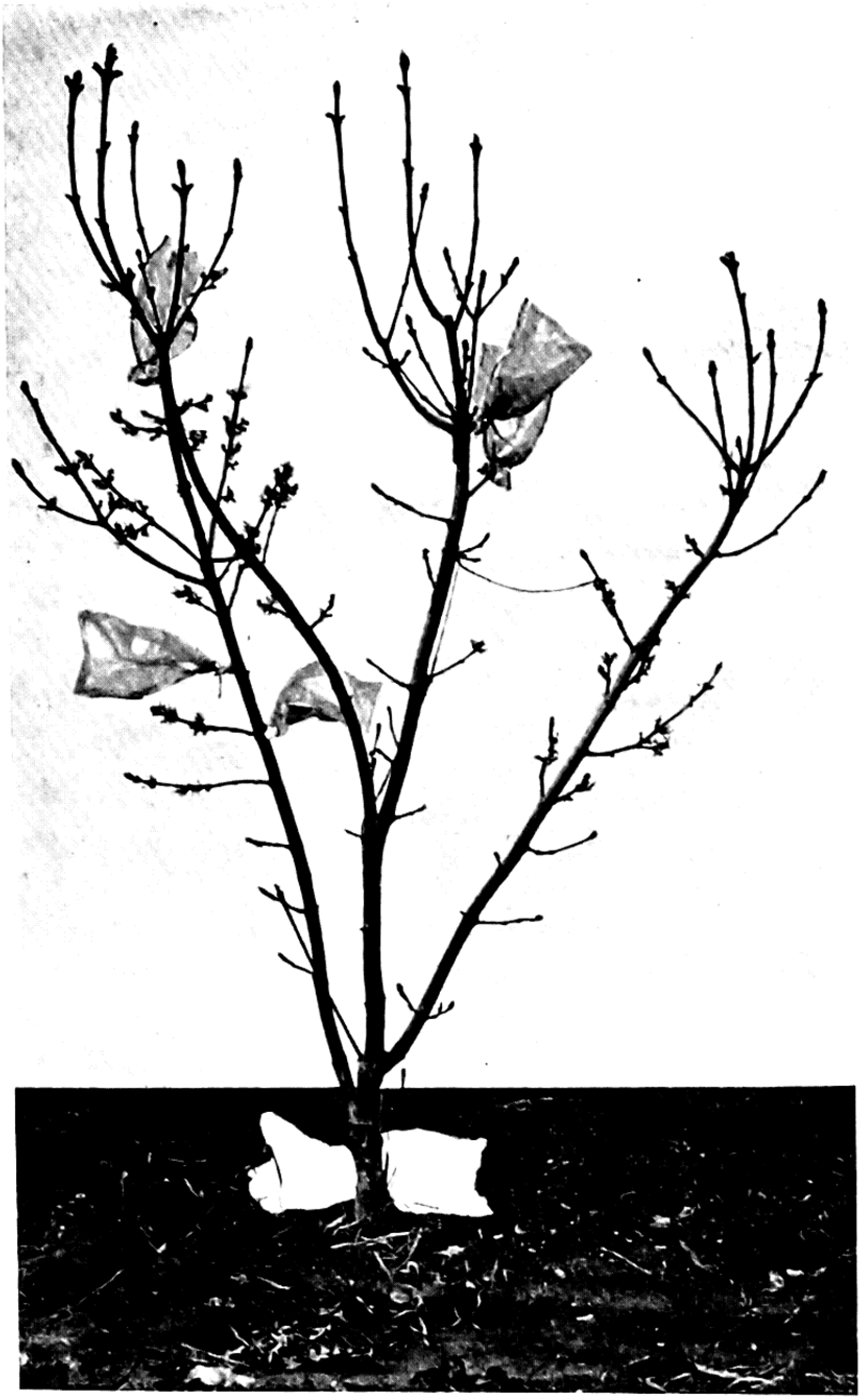

Fig. 21. *Fraxinus excelsior* L. Predominantly male ash. Treated as a breeding tree. Grafted in the spring of 1938; *photo*, Arboretum, 28th April 1943. Those few inflorescences, which also contain female elements, are isolated in paper bags for self-pollination. The main object is to use such a plant as a pollinator in seed-gardens. Phenotype is unimportant.

As another example within the same tree-species, we may mention six graftings of one clone from a rather less heavily seed-producing tree (V.25). These were grafted in 1936, and their seed-setting in the autumn of 1946 consequently refers to their eleventh year. They gave 0·2; 0·3; 0·65; 1·0; 1·2; and 1·45 kg. of seed respectively. This gives on the average 0·8 kg., or about eight thousand seeds per graft.

The year 1946 was favourable for the seed-setting of ash, so the figures are high. A third clone of ash from a particularly heavily seed-bearing tree gave as much as 3·5 kg. of seed on a twelve-year-old grafting. Apart from the seed-year being a good one, it must be admitted that the figures refer to only a few examples, so that here again nothing can be said about what is to be expected in a single year. The figures very clearly show, on the other hand, that even quite young graftings can bear considerable quantities of seed, and not very many graftings should be needed for them to be able to produce in combination a quantity of seed exceeding the yield from even a large and broad-crowned tree.

As regards the problem as a whole there is, one hopes, enough evidence to show that we can confidently set about the establishment of seed-gardens. A seed-garden of ash established in this country, planted in 1947 with one- and two-year-old graftings and buddings, in 1953 gave in all 77 kg. of seed. The area is 3·2 ha. (7·9 ac.), the spacing being 4 × 4 m. (13 × 13 ft.). One-half of the plants are " pollinators ".

The establishment of seed-gardens is most appropriate for coniferous trees, which are characterized by bearing many seeds from a single tree. They are also suited, however, for a number of leaf-trees, of which *Fraxinus* (ash), *Alnus* (alder), and *Betula* (birch) may be mentioned as examples for which experience is available. Undoubtedly it will also apply to many other, especially tropical tree-species. It will be less popular for species like *Quercus* (oak) and *Fagus* (beech) with large seeds in small numbers, and particularly for those in which the seed-setting begins later. With these, larger areas and longer waiting periods must be expected, but here too there must be progress.

Seed-gardens will be of special importance for the production of hybrid seed. They are the technical aid which renders possible the utilization in forestry of hybrids with an accurately known composition.

The very promising *Larix eurolepis*, the hybrid between Japanese and European larch, certainly readily puts in an appearance where the two species are planted near to one another, but in such cases there has been no opportunity of controlling the pollination. Things are better in a seed-garden, where it is known in advance what value the clones employed have, or in which a single clone is planted out for pollination from seedlings raised from the other species by controlled pollination. There are fresh opportunities for variation in the lay-out of such seed-gardens in order to obtain a crop of seed for the valuable F_1* plants. There will not merely be a question of hybrids between the species, but also of hybrids between " types " within the individual species. (See further under " hybrids " and in the chapter on " genetics ".)

The term " seed-garden " (seed-orchard, seed-plantation, or seed-source-garden) should be used only for establishments which are laid down with improved seed-production in view. Broadly speaking that will mean that it ought to be applied only to plantations in which plants vegetatively reproduced (clones) or seedlings are used which have been raised after controlled pollination and have most frequently been the subject of selection.

Although existing growing stands can be particularly valuable for seed-production, they ought not to be included under the name, but should always be referred to as " seed-stands ". The same applies to plantations for which seed has been used from selected trees derived from free, uncontrolled pollination. However valuable and satisfactory that may be, it seems to me, nevertheless, to approach very near to ordinary good afforestation. Seed-gardens, as well as forest-tree breeding as a whole, ought to have their roots in reliable knowledge obtained from controlled pollinations and vegetative reproduction in clones.

That may perhaps only seem to be a splitting of hairs, but it is more than that. It is important to keep the concepts distinct from each other. After having mentioned the necessity for controlled pollination, I said in the publication *Forest Tree Breeding* (Royal Veterinary and Agricultural College, Copenhagen, 1934, pp. 111–112): " Vegetative propagation, however, should not be undertaken solely for the purpose of future preservation and experimenting; it should also be made to serve a more direct practical purpose, inasmuch as the graftings and cuttings may be planted in specially isolated places, and thus be protected against outside pollination in such a way as to produce seeds from desired pollinations in great quantities." It is my opinion that the two things must together provide the basis of our future seed-gardens, and that is, in fact, broadly speaking, the way in which it has later been taken up in forestry. Difficulties at the start must not persuade us to reject the idea.

Isolation of the seed-gardens is a serious problem. When siting them it is very natural to do so by first taking into consideration the ease with which the pollen is spread by the wind. This may seem a very difficult matter, as there are investigations which show that pollen is scattered widely around. There would, however, be a very great difference in having a seed-garden completely protected against strange pollen, and having it located in such a manner that pollen from outside is of secondary importance. If in a seed-garden there is abundant opportunity for the timely and continuous pollination of the female flowers, the pollen from outside will not then have much chance. Merely by taking quite modest precautions for isolation it will occur in relatively moderate quantities.

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* First generation, following a cross.

Within a restricted range, as, for example, the area of a research station, it will certainly be difficult to find room for more than one, or at most a very few, seed-gardens of each tree-species. On the other hand, on any one area at our disposal a whole series of seed-gardens can be grouped together, provided that they are of different species, which are not susceptible to mutual crossing. By confining oneself only to different *genera* such as *Pinus* (pine), *Picea* (spruce), *Larix* (larch), *Pseudotsuga* (Douglas fir), *Betula* (birch), *Alnus* (alder), *Quercus* (oak), etc., it is possible to have a whole collection upon a single area.

It would be a good general rule to locate the production of seed outside those areas, where the species of tree concerned are commonly grown or occur naturally. Seed-gardens for leaf-tree species could be located as isolated areas within forests of conifers, and vice versa. It would also be possible to isolate them by scattering their positions about in agricultural areas or on solitary islands. Mention might also be made of areas in protection forests or water-catchment areas, where the exploitation of the forest may be considerably restricted, without there being any need, however, for prohibiting the establishment of seed-gardens.

In Denmark, where forestry uses not a few indigenous and introduced tree-species, the decision has been to scatter the seed-gardens over the country, where they are mostly isolated, and only to link them up in a common organization, which relies to an overwhelming extent upon forests owned by the State.

Establishment of seed-gardens makes great demands upon foresight, and a successful result depends very much upon the possibility of satisfactory co-operation for the common good. On the other hand it is facilitated by the high yield of seed which can be expected from relatively small areas.

Where the conditions allow, it may be recommended that several small areas isolated from one another should be established, as by that method there may be better security than in one large establishment. As establishing seed-gardens in itself does not cost a great deal as soon as one has the material for them, I myself often proceed by laying out several combinations very similar to one another. This is done because it may be difficult now to make the correct decision regarding the use of the seed in the future. Therefore we must rather act boldly and establish an abundance of seed-gardens, so that we can afford to retain only the best.

Before establishing seed-gardens it will be usual to make a collection of scions from the largest and finest trees required for the purpose. When these have been converted at the research station into a suitable number of graftings within the individual clones, planting is carried out according to a prearranged plan, so that the desired pollination is encouraged as much as possible. It is important that the planting should be done as exactly as possible and that careful notes should be taken, so that one can later with complete certainty again find all the specimens in the individual clones. That is necessary for seed collection, and in case it is desired later to introduce a change of conditions in one direction (combination) or another.

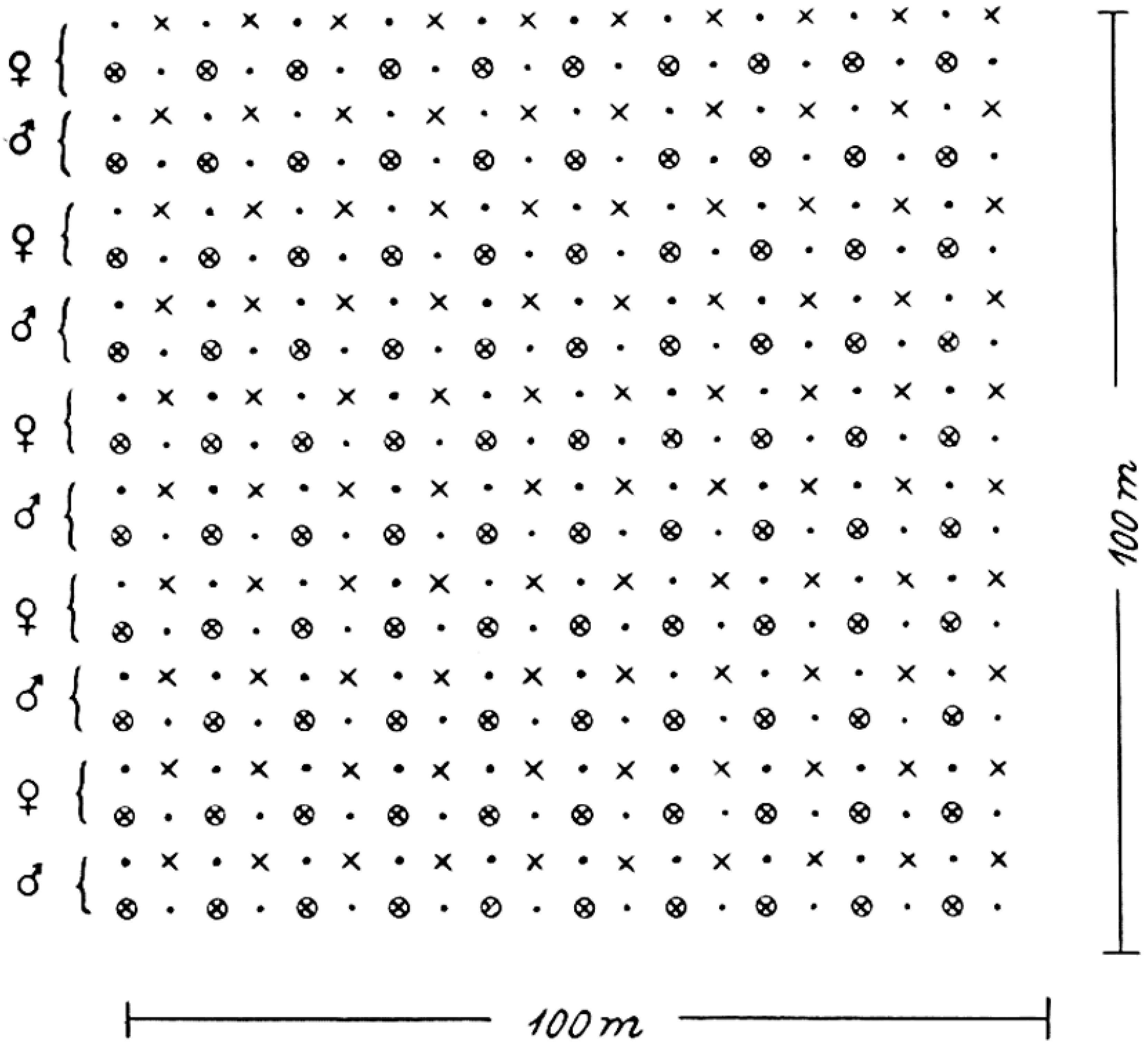


Fig. 22. Diagram of a 1 ha. seed-garden, in which seed-trees (♀) and pollinators (♂) are differentiated. They are planted at 5 × 5 m. (16½ × 16½ ft.). At the first thinning every other tree is removed (marked •), and at the next one the trees marked x. The trees marked ⊗ will then stand at 10 × 10 m. (32¼ × 32¼ ft.), and both seed-trees and pollinators are preserved in equal mixture.

It may sound inviting to postpone the setting-up of a seed-garden until the qualities of the individuals used in it are accurately known. Best use of the time will often be made, however, by establishing the seed-garden with clones after only a provisional appraisement. If there were to be delay until the results of tests made by controlled pollination of the various clones and their combinations were available, much time might be wasted. Broadly speaking, all those clones which may be taken to be of value ought to be included, while at the same time the earliest possible pollinations for testing them should be performed. Gradually, as results become available, those clones behaving in a negative manner can be removed. It is preferable to have a garden full of gaps than to lose time.

The planting distance must be a wide one and the plants put in on accurately measured off and charted planting-places. Planting in double or even in triple rows may be recommended, so that the one or two extra rows can be removed, according as the plants develop. A spacing of less than 3 m. (10 ft.) each way will seldom be capable of offering any advantage. It will often be wise to plant at 4 × 4 m. (13 × 13 ft.), so as to be able later to thin out to 8 × 8 m. (26 × 26 ft.) or 12 × 12 m. (40 × 40 ft.).

If the area is not too inaccessible, it will often be an advantage to plant out the stocks first and to perform the grafting later. In this way it is possible to obtain in advance vigorous and well-rooted stocks, which can be grafted as larger plants, which is better than having to move the plants after grafting. For *Pinus* (pine), *Picea* (spruce), *Larix* (larch), *Pseudotsuga* (Douglas fir), *Quercus* (oak), and *Fagus* (beech) we have experience to show that this is an advantage, where no other factor intrudes.

Where the seed-garden has to consist of a single clone with a seed-progeny raised by controlled pollination as " pollinators ", rather dense planting will often be chosen for the latter. For the pollinating only a small number of plants are required, but on the other hand a rather severe grading of them should often be carried out with a gradual removal of the smallest plants. Rather the same thing will apply where it is only seedlings which go into the seed-garden. In addition, one has to take the trouble to distribute the most promising seedlings as advantageously as possible in order that occasions for later thinning out of the promising plants themselves may be reduced to a minimum.

In addition to the features of seed-gardens already referred to, it should also be stressed that it will be a considerable advantage to have the seed-production concentrated on definite areas, as this makes it easier to devise special measures to bring about more abundant and better seed-bearing. Moreover, in this way the collection of the seed may be appreciably facilitated.

It is not unimportant that the seed may be better nourished, so that it has the greatest possible store of food, and we can contribute to that by suitable treatment such as a favourable climate, pruning of the plants, and manuring. The size of the seed is to a great extent determined genetically, but it is without doubt also susceptible to good treatment.

In the first place, however, we are anxious to get early and abundant seed-setting. In order to achieve this, in fruit-breeding it is quite often the practice to girdle the trees. I would not recommend this except in very special circumstances. I believe that our experience shows that all the conifers suffer too much from that procedure for it to be applied in seed-breeding. With the leaf-trees there is greater opportunity, but it has to be performed with great care. It has its greatest importance when one can spare some specimens to obtain a particularly abundant seed-setting in a certain year.

It would seem to me to be better to make use of a moderate root-pruning, as each plant can be conveniently pruned by itself. Attention must also be directed to appropriate nourishment, which may possibly promote seed-setting. The proportion of phosphorus to nitrogen is significant, since an excess of phosphorus may be stimulating for seed-setting. We lack much information about this, however, and we still have a good deal to learn from fruit-breeding and other fields. On the assumption that it may be easier to apply to the soil missing food-stuffs than to absorb any excess, it may be an advantage to plant seed-gardens on relatively light soil.

Applying nutrients and other treatment, which we can control in a seed-garden, must also be of significance in the important problem of a more regular annual seed-setting. The majority of our forest trees are characterized by producing large quantities of seed in individual years, whereas a varying number of intervening years may be completely or almost completely devoid of seed. About the causes of that, and the possibilities for altering the conditions affecting it, we know but little; but it may be said with certainty that the seed-gardens will also make it possible to use experience, as soon as it happens to be acquired. They will lend themselves directly to researches in this field.

The climate in itself must be an important factor, not only for the commencement of flowering, but also for the further development and ripening of the seed. Under exposed conditions such as occur in the far north and high up on mountain slopes it is a well-known observation that " seed-years " are rarer than under more favourable conditions. In order to obtain the best seed for use under these extreme conditions, it is very likely that seed-gardens will prove very helpful. The recommendation may be made to take scions from a number of specimens of the best trees under such exposed conditions, to transform them into clones and to establish seed-gardens from these in the most favourable climate to which they can submit to being transferred. If they can be isolated there, so that only mutual pollination will come into effect, a yield of seed will be secured with the same genetical characteristics as if a controlled pollination had been performed between the most desirable trees in the natural stand from which they originated. Because of the position of the seed-garden in the more favourable climate, the seed produced will have the best opportunity to develop without climatic disturbances, just as they will have a better chance to build up a valuable store of food. Of two pine seeds with the same genetical tendencies, the seed with the largest store of food (seed proteins) must give the strongest one-year plant and thus the one with the best start in life. This point is of great importance. It must, however, be kept distinctly separate from the problem of the raising of seed on seedlings which have been subjected to such a climatic transfer. That is something very different, because through it a displacement of the inherent tendencies may be brought about in the seed produced in the more favourable climate, which cannot therefore be recommended for transfer back to the original source.

With further experience there is a possibility that the question may be taken a stage farther to refer also to the more general supply of seed. It is possible that, by climatic transfers of our seed-gardens or by establishing them under different climates, perhaps combined with artificial interference, an appreciable contribution may be made to a more uniform and more abundant supply of seed.

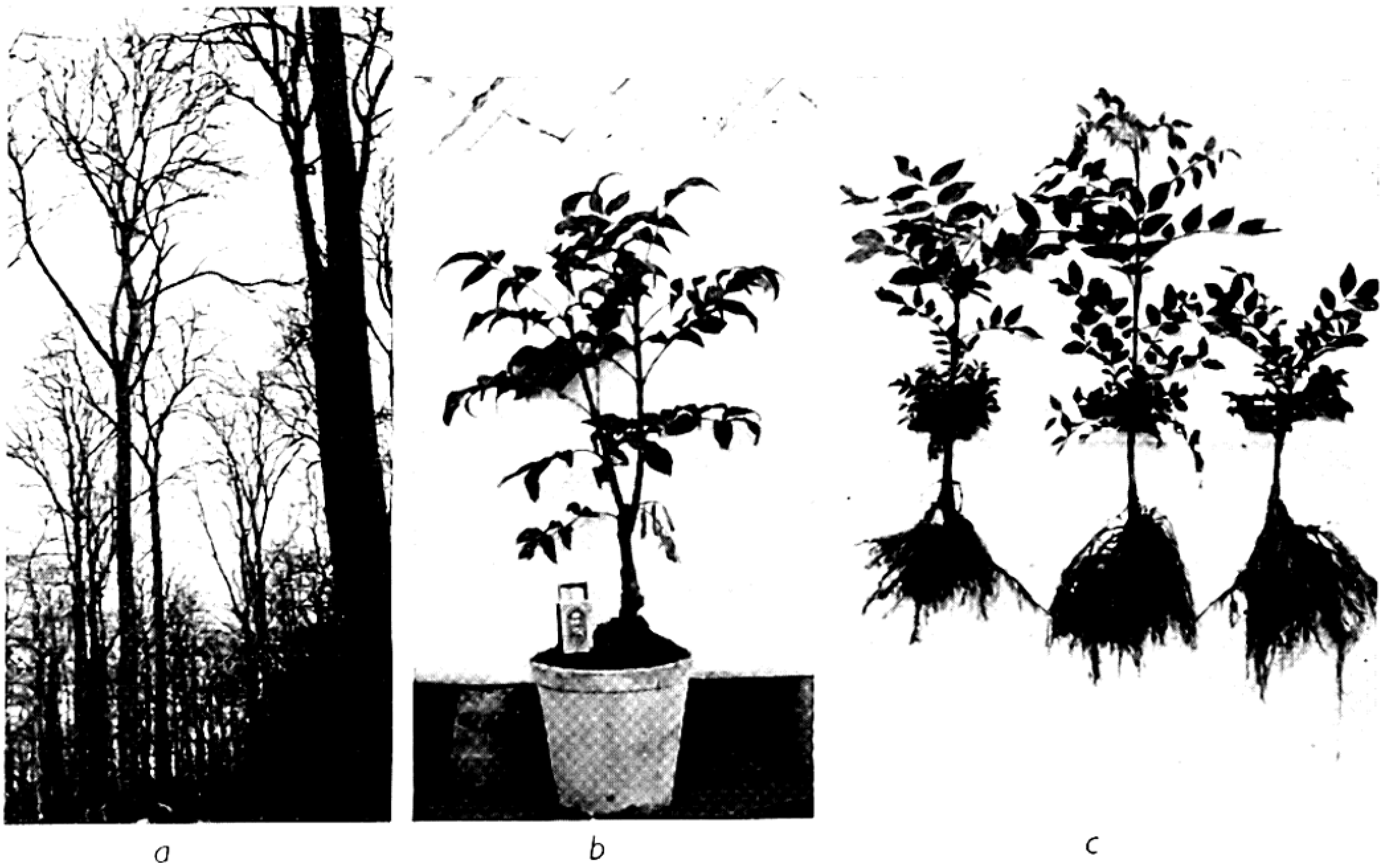


Fig. 23. *Fraxinus excelsior* L. Quick result from a small "seed-garden". (Clone V.282.) (a) The fine, old ash, which was just on the point of being felled, photographed on 14th February 1938, at which time scions were collected. (b) One of the graftings with seed in the greenhouse, 22nd August 1939. (c) Seedlings from the seed in Fig. 23b, germinated in 1941. *Photo*, 25th September 1942.

Until there is further experience in this field, we should stick to the establishment of such an abundance of seed-gardens that an excess production can be ensured to make good any expected " barren " years. It is possible to store the seed from a number of trees over so long a period of years that intervening barren years can be made good in that way. This applies in the first place to many economically important conifers. After careful collection, cleaning, and dehydration to a low moisture-content, they can be kept in store-rooms where a low and constant temperature is ensured.

Besides being of value for the seed produced in seed-gardens, artificial storage of seed is the most important means of supplying the best possible seed earlier. In the heavy seed-years there is no difficulty in the supply of seed from good stands, which can be selected as desired. In the poor seed-years, on the other hand, there may be a strong temptation to reduce the standard in respect of the derivation of the seed—perhaps to make use of seed from a foreign country without knowing whether that would be justifiable. It is of great importance for improved supply of seed to be familiar with artificial seed-storage and to have adequate establishments available for storage purposes. These are the means of avoiding the use of poor seed in the difficult years, and in the event of sufficient production from the seed-gardens they will be the means of placing us in a position of still greater freedom. In Danish forestry the problem has been solved by the State Forest Service's foundation of a plant-breeding station, which works in the closest contact with the experiments at the Arboretum in order to devise methods of forest-tree breeding.

Work with small grafted plants in greenhouses is a special kind of seed-garden. With a number of forest trees, as for example with *Larix* (larch), *Pinus sylvestris* (Scots pine), *Pseudotsuga taxifolia* (Douglas fir), *Fraxinus excelsior* (European ash), *Betula* (birch) and *Alnus* (alder), which we have worked with in the Arboretum, it is already possible to bring about seed-setting on small grafted plants in the greenhouse. We operate with a number of small closed glass-houses of about 3 × 6 m. (10 × 20 ft.) of ground space and 2–3 m. (6–10 ft.) in height. The grafted plants, being in pots, can be lowered into the soil directly and moved in and out as desired, so that they remain in the house only for pollination, but can later be moved out so as to bring the seed further on towards ripeness in the open. The glass-houses, " the pollinating cages ", are without heating, but the closed glass-house by itself will bring about a rather earlier flowering than in the open, which also contributes to isolation. Even the few plants which are able to find room in such a glass-house can furnish quite a considerable seed-yield, which may provide much information for later seed-gardens. In its way it is a small " seed-garden ", from which we have derived much satisfaction. Their extended use may be recommended. Fig. 23 may be referred to as an example of the rapid results which can be secured in this way.

As a contrast to this, another procedure may perhaps be described, in which one avoids, or at least temporarily departs from, the normal establishment of seed-gardens. That applies when the whole crown of a large tree is altered by grafting. This is to be recommended for species in which seed-setting begins late in life. Amongst Danish forest trees it can be of special im-

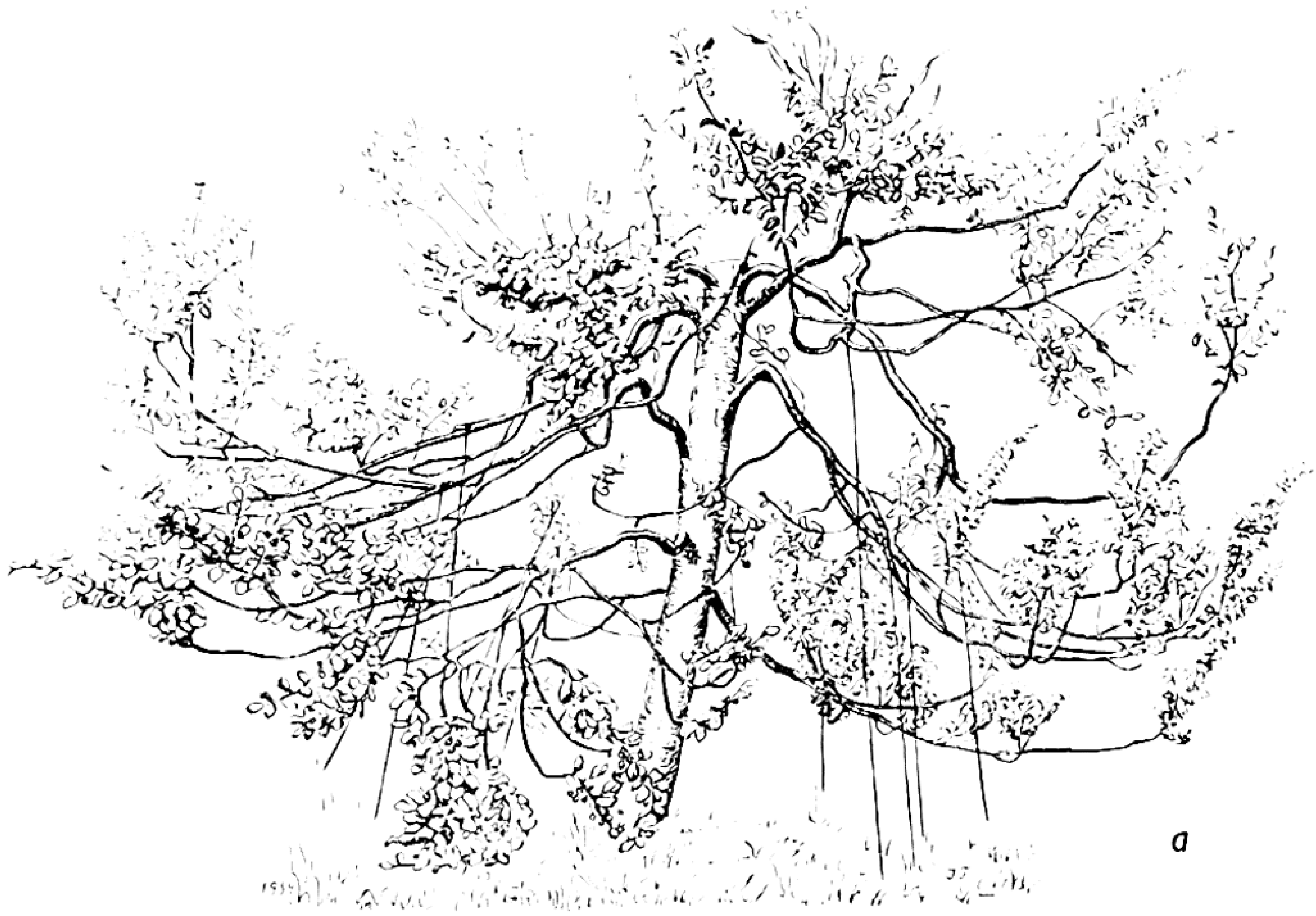


Fig. 24. Grafting on a beech about 50 years of age.
(a) Top and branches cut severely back. Grafting with 5 selected clones in May 1952.

(b) One of the clones was cut directly from branches which had earlier flowered strongly on an old tree. All the graftings of this flowered and gave seed in 1954. The drawing shows one of the branches with seed. Both drawings were made in September 1954.

portance for beech (*Fagus sylvatica*), which even under favourable conditions cannot be expected to set seed earlier than about thirty to fifty years of age.

By grafting beech on to young stocks one can get, in a few exceptional cases only, successful production of a few female or male flowers at an early age. Success was achieved by the cutting back of the crown on an isolated, broad-crowned beech about fifty years of age, so that all the remaining branches could be grafted with the desired clones. This is strongly reminiscent of the gardener's " top-working " of old fruit-trees and may perhaps furnish us with an even earlier seed-setting. In the case mentioned, five different clones were used. (M. SCHAFFALITZKY DE MUCKADELL: " A Development Stage in *Fagus sylvatica* Characterized by Abundant Flowering ", *Physiologia Plantarum*, 1955, Vol. 8.) When carried out on isolated standing trees, these might be called small seed-gardens. See Fig. 24.

Besides having a late seed-setting, beech is difficult to graft, so that it is generally necessary to carry out a severe pruning of the scions. The aim must be to transfer by grafting as much as possible of the branch ripe for seed-setting to the older stock. There one can then undertake further opera-

b

tions in order to bring about the best possible relationship between the new crown and the old stock to promote—or maintain—seed-setting. There is a wide field for further research into this question.

Beech is, however, one of the exceptional trees, but even for it we can to-day proceed to establish seed-gardens, in which we have only to wait longer on the results than with other tree-species. For the great majority of forest trees, rapid and certain results can be anticipated by the use of vegetative propagation in establishing seed-gardens.

The work must proceed hand in hand with the making of controlled pollinations, which must give the decisive answer to the question of seed-quality. In order to gain time, however, we must not await the results of the pollinations. We must straight away choose the largest and finest trees at present existing in the forest for vegetative reproduction and allow them entry into the seed-gardens. Of these the poorest can later be removed, as soon as the result of controlled pollination is evident. After that only the most valuable trees will form the final seed-garden.

Our selection of the trees for breeding must in the beginning be made on a rather slender basis. In the forest we can only select trees which have become satisfactory under the conditions which happen to exist. We have very little opportunity to assess what were the conditions which have helped them to become the best and dominant trees. These trees have demonstrated, however, that with their inherent tendencies they have been able to become valuable individuals. Already the fact that it is possible to harvest seed deriving from a mutual pollination of these trees must be regarded as being a great step forward. To this will be added the later more intensive selection, as soon as the result of controlled pollination is available. Opportunities also exist, however, through direct observation of the individual features of vegetative propagations, to procure a basis for an evaluation of the material. This will be dealt with in the following pages.

CHAPTER VII

TREE-SHOWS

THE breeder of herbaceous plants does not bother about assessing the inherent tendencies unless the plants have grown up under as uniform conditions as possible. If he wishes to compare plants which are living under different conditions, he digs them up and brings them together under so far as possible identical conditions, before attempting any evaluation of their respective merits.

The forester does not have much interest in comparing young plants which can still be moved. As his basic information he should have an evaluation of the innate tendencies of large and well-developed trees, which do not lend themselves to being dug up and moved. Once again vegetative propagation comes to our aid in this connection. It makes it possible for us to distinguish still more clearly between phenotype and genotype.

" Tree-shows " are groups of plants produced vegetatively, in which each group represents a single tree—a single clone—and they are laid out in such a manner that mutual comparisons can be carried out. The use of tree-shows has proved to be of considerable help in appraising the genotype of trees.

W. JOHANNSEN introduced the concepts of genotype and phenotype and was the first to stress the importance of distinguishing carefully between them. This became of great significance in improvement work, in which quantitative heredity was being dealt with. The genotype is what is inherited from the parents, whereas the phenotype is the result of the reaction of the genotype to the given external environment.

In the case of forest trees the phenotype is determined by the environment in which they have grown up, and which alters in the course of time. On account of their size, their deep-going roots, and great ages, trees must be regarded as being subject to external effects to a greater degree than other plants. We have very little hope of being able to provide ourselves with information about the conditions which have moulded the tree for the past fifty or one hundred years. It is therefore difficult to select trees to provide a basis for breeding according to the phenotype which we find in the forest. Many are aware of this fact, and they stress that an assessment of the progeny is the only workable procedure.

As the life-history of most trees covers many years, and controlled pollination presents difficulties, satisfactory assessment of the progeny is a troublesome and prolonged procedure. We must therefore make use of every means which contributes to an easier assessment of the genotypic composition of the individual trees. In order to save time and money we must try as quickly as possible to arrange for a grading based on an examination of the material collected according to the phenotype. In this, tree-shows are a valuable help.

It must be remembered that this will be only one step on the path towards improvement. Forest trees, being pollinated by the wind, must in all probability be most often markedly heterozygotic in their tendencies. We cannot get away from the progeny assessment, but we can narrow it down considerably. It is the next step ahead towards finding the best trees for breeding. We must not be annoyed, however, because we cannot leap the whole distance to the best breeding trees at a single bound.

The French botanist GASTON BONNIER " divided up " a plant of *Taraxacum* in order to be able to grow the different parts under lowland and alpine highland conditions respectively, thereby providing himself with a basis for judging the influence of the climate. (Concerning this see GASTON BONNIER, 1895, in "Recherches experimentales sur l'adaption des plantes au climat alpin," *Annales Sciences Naturelles*, Ser. 7, botanique, Vol. 20.) We can divide up our trees in the same way and use them for similar tests under different conditions; or we can take parts of trees, grown under different conditions, in order to compare them on the same area.

Reference may also be made to the gardener's use of numerous garden forms, the so-called " varieties " of ornamental trees. These are neither ecotypes which have arisen naturally, cultivated plants (sorts) true to seed, nor in any other respect varieties in the true meaning. They are all only vegetative propagations from individuals which have arisen by chance, having a peculiar combination of inherent tendencies; they are plants of odd genotypes.

The majority of these garden forms are reproduced by grafting on stocks which are unselected seedlings, most often of the species in question, and they have become very widespread. Every gardener knows how to cut scions to take home for his own use.

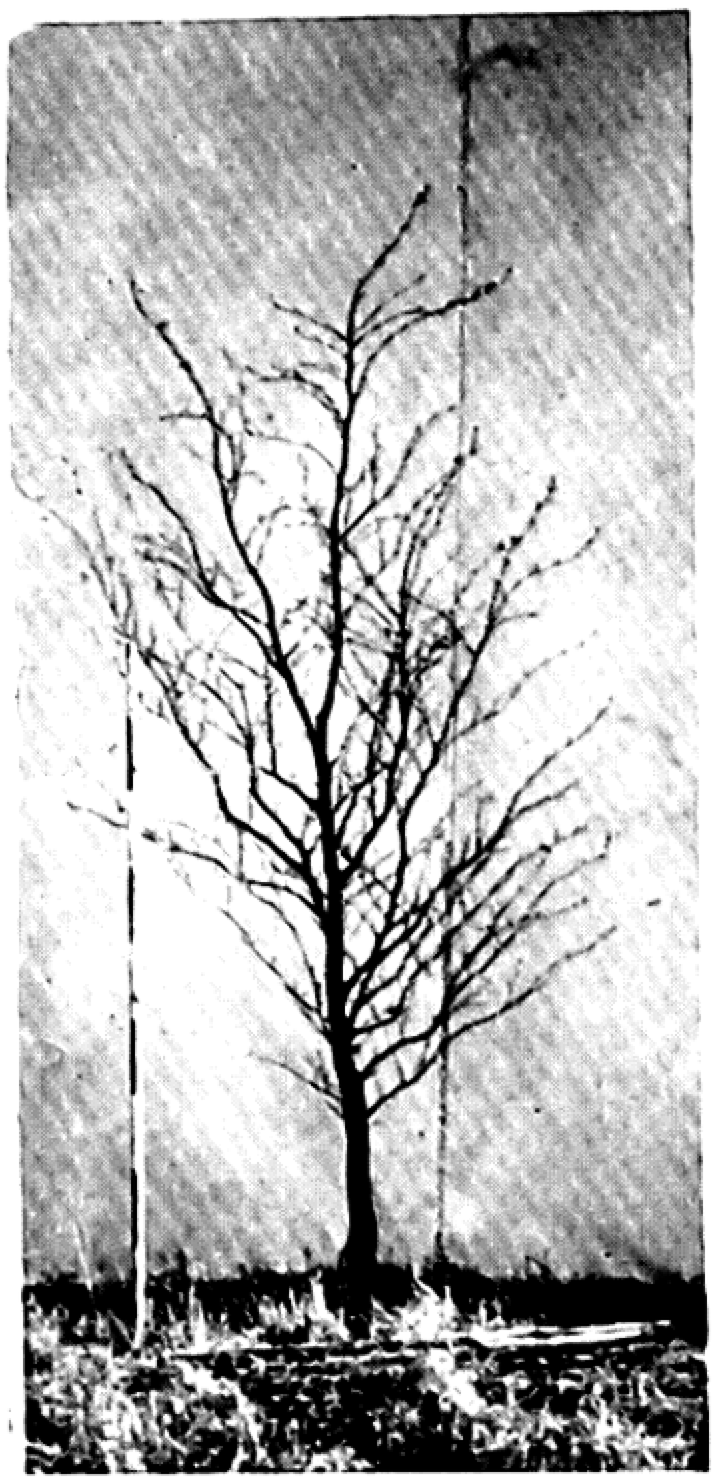
Such a genotype (clone), whether it be a weeping beech (*Fagus sylvatica* var. *pendula*), or a snake spruce (*Picea Abies* var. *virgata*), is easy to identify scattered throughout European and American parks. Similarly we find

Fig. 25. *Beech* (V.262). "Tersløse Forest". (a) Original tree photographed 18th November 1937. (b) (c) Grafts of 1938, photographed in January 1947.

Fig. 26. *Beech* (V.263). "Tersløse Forest". (a) Original tree photographed 18th November 1937. (b) (c) Grafts of 1938, photographed in January 1947.

a

b



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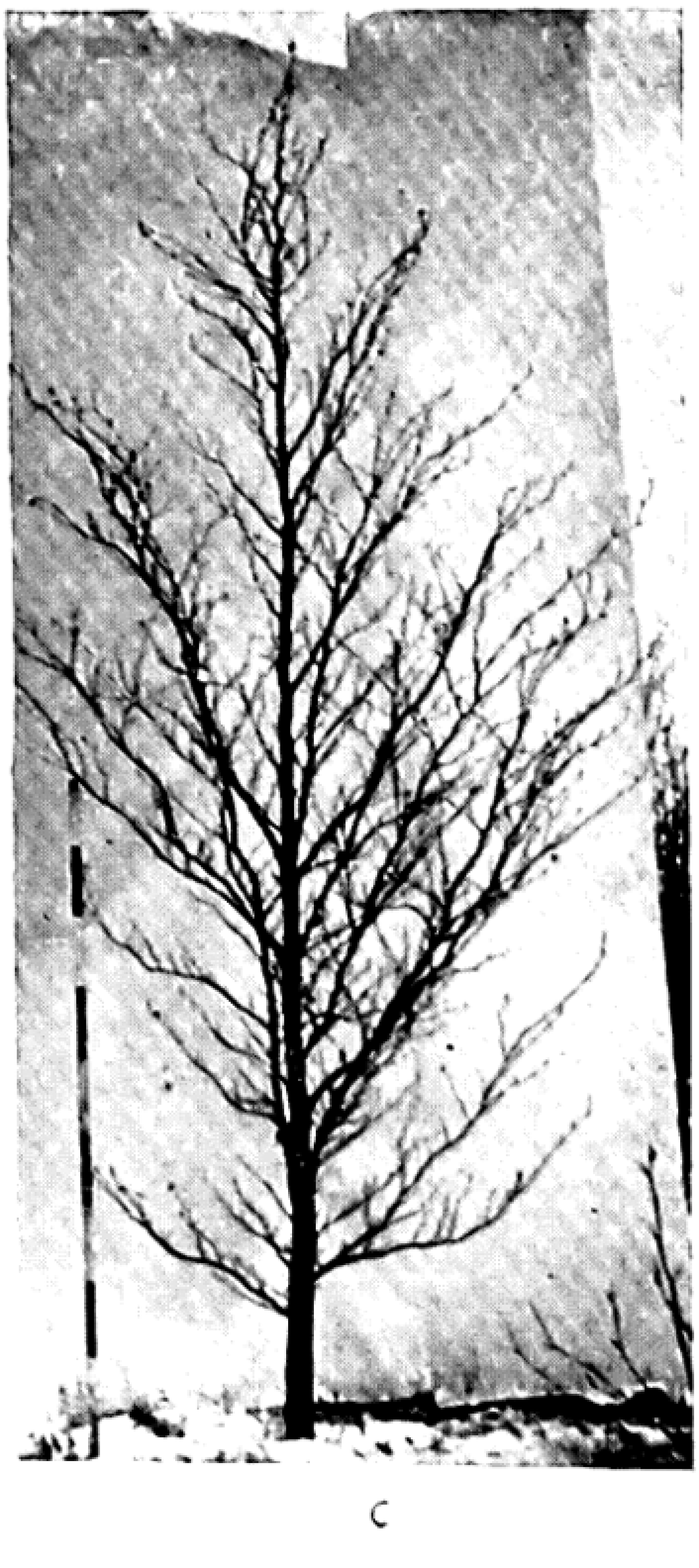


c

peculiar genotypes (clones) distributed from Japanese and Chinese gardens over the rest of the world, wherever any tree-species can thrive at all, without being able to observe the slightest change (*Cryptomeria japonica* var. *elegans*, *Chamaecyparis pisifera* var. *squarrosa*, and many others). A very large number of garden forms exist without its being possible to see any difference, which can be attributed to the influence of the stocks or growth of the cuttings under very varied conditions. If we take into account how uniform individuals of the same garden form are from place to place, we shall be astonished how it is possible to go more and more into details and always find agreement in respect of branching, leaves, buds, flowering, and much more. It is quite true that such trees very often stand in isolation and unencumbered by other trees standing near them; but even when circumstances are otherwise they will not change their characters to any extent. Very often they will succumb in competition with other trees, just because of their inability to alter their growth-form. But before the weeping ash is over-shaded and killed off by other trees, it does not lose its character of being a weeping ash.

If we think this question over we shall find it quite natural that such garden forms should be of exactly the same appearance, wherever we encounter them, as they have all been derived from twigs (parts) of one and the same individual. All that is lacking is to carry the idea farther and transfer it to other trees which, to the forester, are far finer and economically much more valuable.

In forest-tree breeding we should not concern ourselves with strange " freak " trees, but on the contrary with trees which are competing to be the largest and finest in the forest. It is therefore more apposite to look at the use of certain garden forms in avenues and similar plantations, where uniformity has been sought after. References may be made to forms of elm such as *Ulmus hollandica* var. *Wheatleyi*, *U. hollandica* var. *vegeta* (Huntingdon elm), forms of lime, plane, and others, which are sometimes raised by grafting and budding and sometimes by cuttings; or we can look at poplars closely related to one another, in which each of the various forms (clones) has its characteristic growth-form.

Such varieties often differ so slightly that the difference is not conspicuous when they are seen only as individual specimens. When each of them is seen by itself in the mass, as, for example, in avenues, one becomes struck by the uniformity of the individuals and the mutual divergence between the clones. It is therefore an urgent matter to investigate how far we can go towards comparing the inherent tendencies of trees chosen because of their forestry qualities.

Over a number of years, at the Arboretum at Hørsholm, we have worked with our forest trees in the form of vegetative propagations, from a desire to achieve, so far as possible, *a uniform phenotypic effect upon several genotypes*. These are our "tree-shows".

It might seem obvious to assume that for such research work use should be made only of cuttings, in which the clone also comprises the root. This is so in the case of poplars, and it has been used by M. L. JACOBS and J. M. FIELDING for *Pinus radiata* (Monterey pine) in Australia. In the latest published paper, FIELDING reports a long series of important observations in the Australian experiments with cuttings of *Pinus radiata*, referred to in detail on page 212.

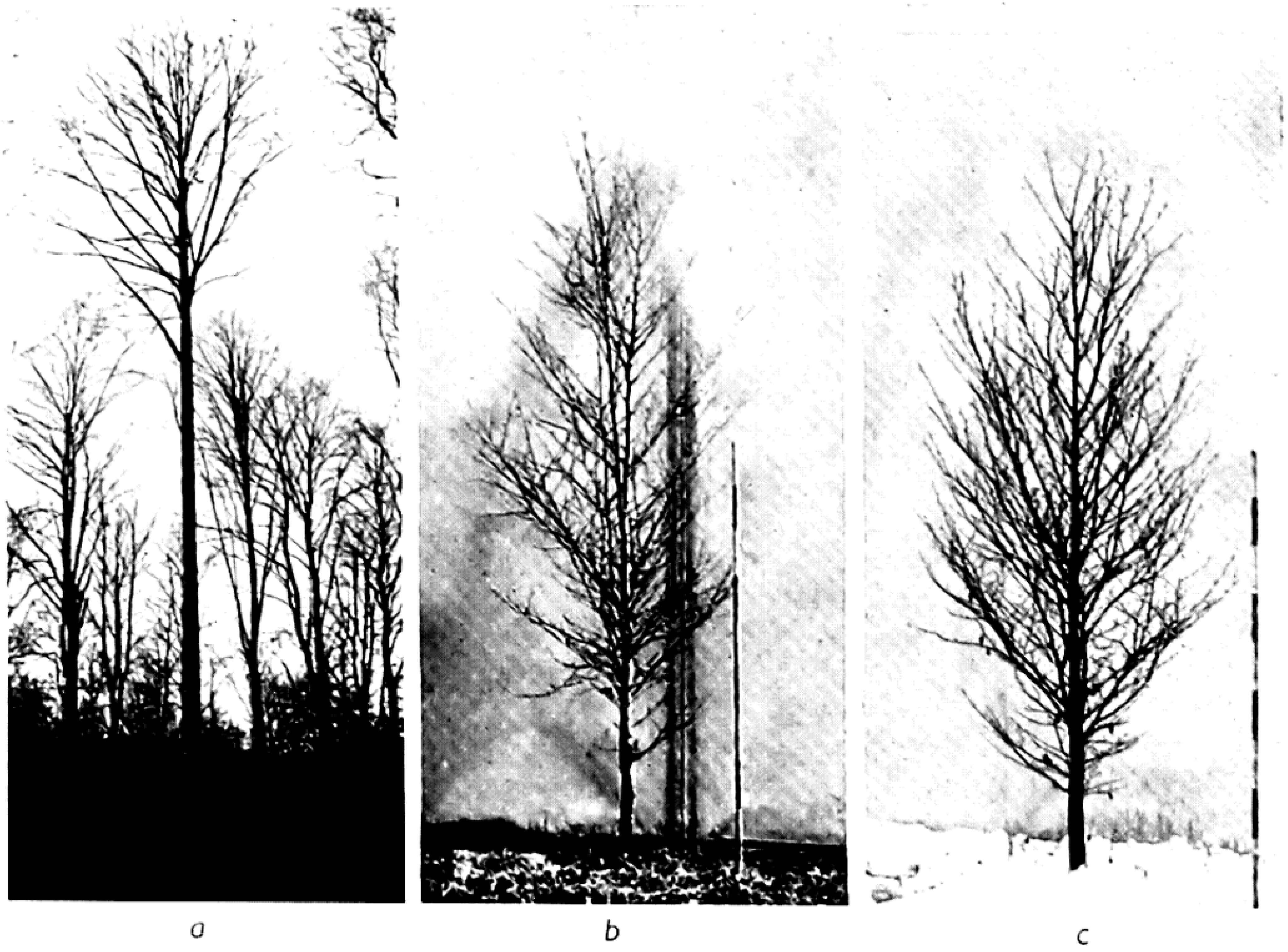


Fig. 27. *Beech* (V.265). "Orebo Forest". (a) Original tree photographed 18th November 1937. (b) (c) Grafts of 1938, photographed in January 1947.

It is a work which should arouse interest, and it proves that much may be obtained by rather small and comparatively short-term experiments. The method may be directly used in other species which can be propagated by cuttings in the same way as *Pinus radiata*.

However, by far most of the important forest trees of the northern hemisphere are more easily propagated by grafting than by cuttings. Therefore the question of the use of grafts is of great interest, and many experiments with grafts have been made here.

By using graftings from selected trees we have obtained such remarkable uniformity within the " clone " that it must be taken to indicate that the foundation (the root) has been of small importance. It may also be put in this way, that the different clones show such large mutual differences that, by such a comparatively crude test as grafting on a collection of seedlings, they are still in a position to show a genotype characteristic of the scion (clone).

By using a more uniform foundation it is perhaps possible to obtain finer nuances. Should it not be practicable to work with cuttings, the solution is perhaps to produce a genetically uniform foundation, such as is used for several fruit-trees. Thus uniform plant-lots will be obtained in such a way that root and top are each by themselves mutually homogeneous. In this connection it must be remembered, however, that a great deal of work lies ahead before clones are used as root-stocks in fruit-breeding, where it was only after prolonged researches that success was achieved in demonstrating and utilizing the capacity of the stocks to affect the clones grafted upon them. Nor must it be overlooked that vegetatively reproduced stocks, in spite of the ancient employment of grafting in gardening, are used only to a small extent. We need look only at roses, where the individual clone (sort) appears to be uniform in all details, although it is budded on seedlings.

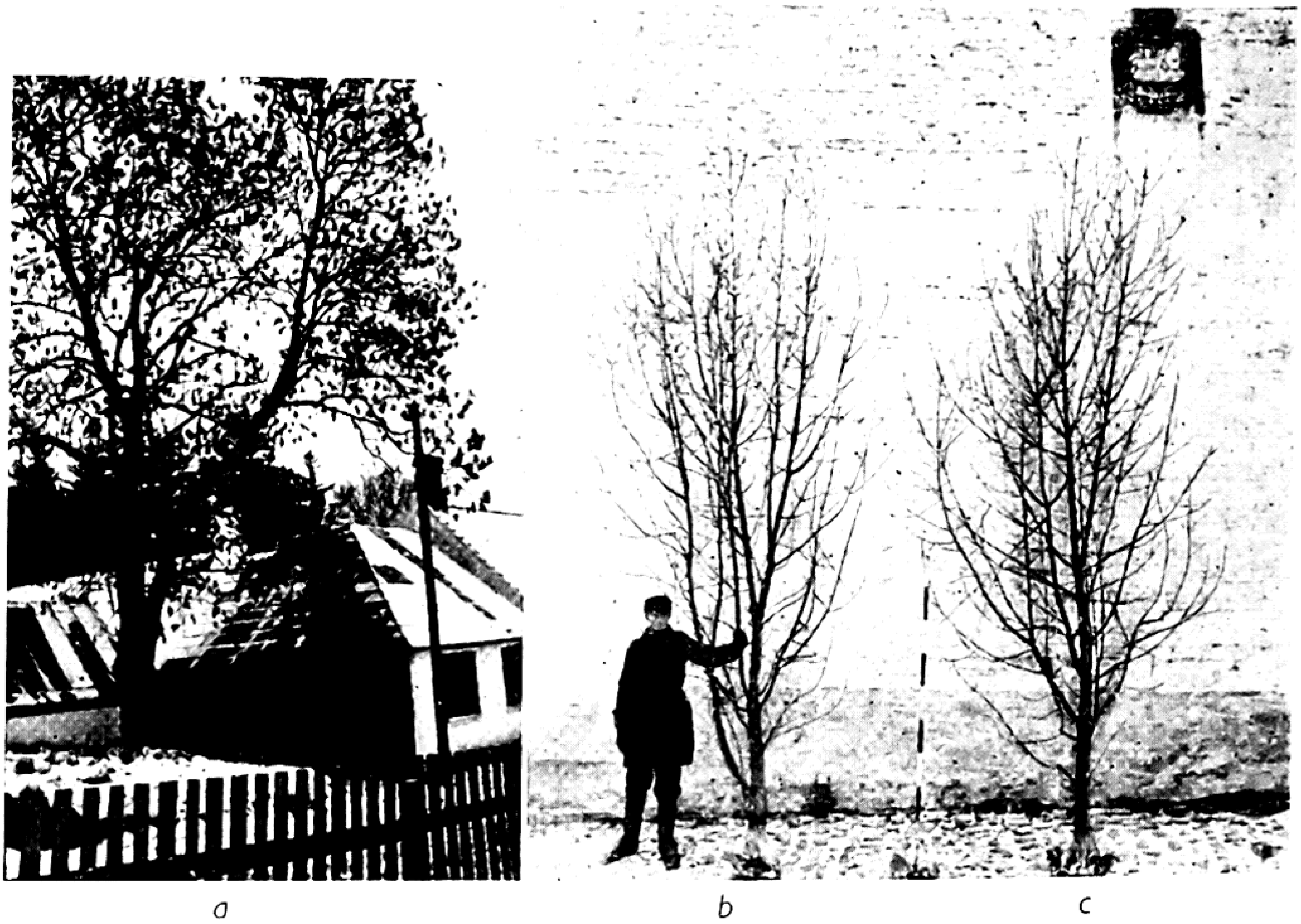


Fig. 28. *Ash* (V.4), Linaa. (a) Original tree photographed in January 1947. (b) (c) Grafts of 1935, photographed in December 1946.

In grafting for tree-shows we should, just as in other grafting, use stocks of a single species and in healthy uniform lots. It will be quite another matter to try the individual clone on different stocks in order thereby to achieve earlier seed-setting or some other benefit. The two things simply must be kept separate.

From observations in the forest we get an idea of how a tree-species varies. We see, however, only individual trees of different form and appearance, and we can only guess what may be due to inherent tendencies. It is entirely different when, by vegetative reproduction, we have produced from each of the observed trees a number of individuals, and these remain identical with one another, so that the clones can be compared by rows. From our experiments it is striking how great are the diversities which can be discovered between individuals within the same species and stand. Provided they are grown in rows for observation and comparison, it is astonishing how it is possible to discover more and more detailed differences.

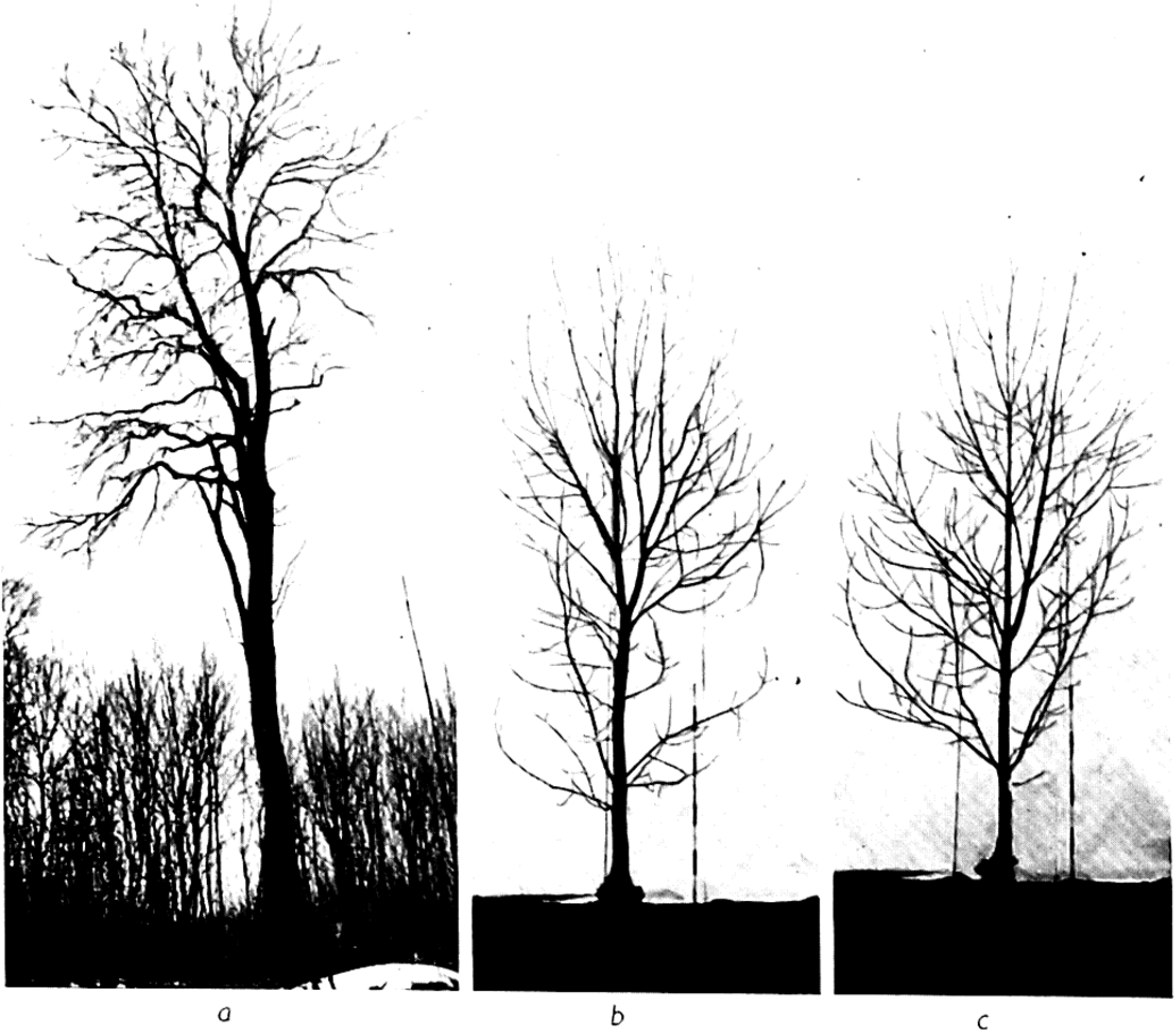


Fig. 29. *Ash* (V.25), Havnø. (a) Original tree photographed on 4th March 1936. (b) (c) Grafts of 1936 photographed in December 1946.

Establishment of tree-shows is therefore an important task in forest-tree breeding in order to make progress towards an assessment of the genotype—the characteristics determined by inherent tendencies.

This should become clearer from several examples now to be described. (Cf. C. SYRACH LARSEN: "Estimation of the Genotype in Forest Trees," *Royal Veterinary and Agricultural College, Copenhagen, Yearbook*, 1947.)

For beech (*Fagus sylvatica*) we may choose three clones: V.262, 263, 265. These represent three fine trees, which on the basis of their appearance (phenotype) in the forest were selected as subjects for breeding. These were taken as three of the best trees in a particular forest district (Sorø II). They were all grafted in the spring of 1938 on small seedlings in pots in a greenhouse, and were later handled as uniformly as possible. They were transplanted into the Arboretum at a spacing of 0·8 × 2·0 m. ($2\frac{1}{2} \times 6\frac{1}{2}$ ft.), but only a small number of the best-developed graftings could be retained afterwards. The remainder fell victim to constant thinnings and use of the material for further research.

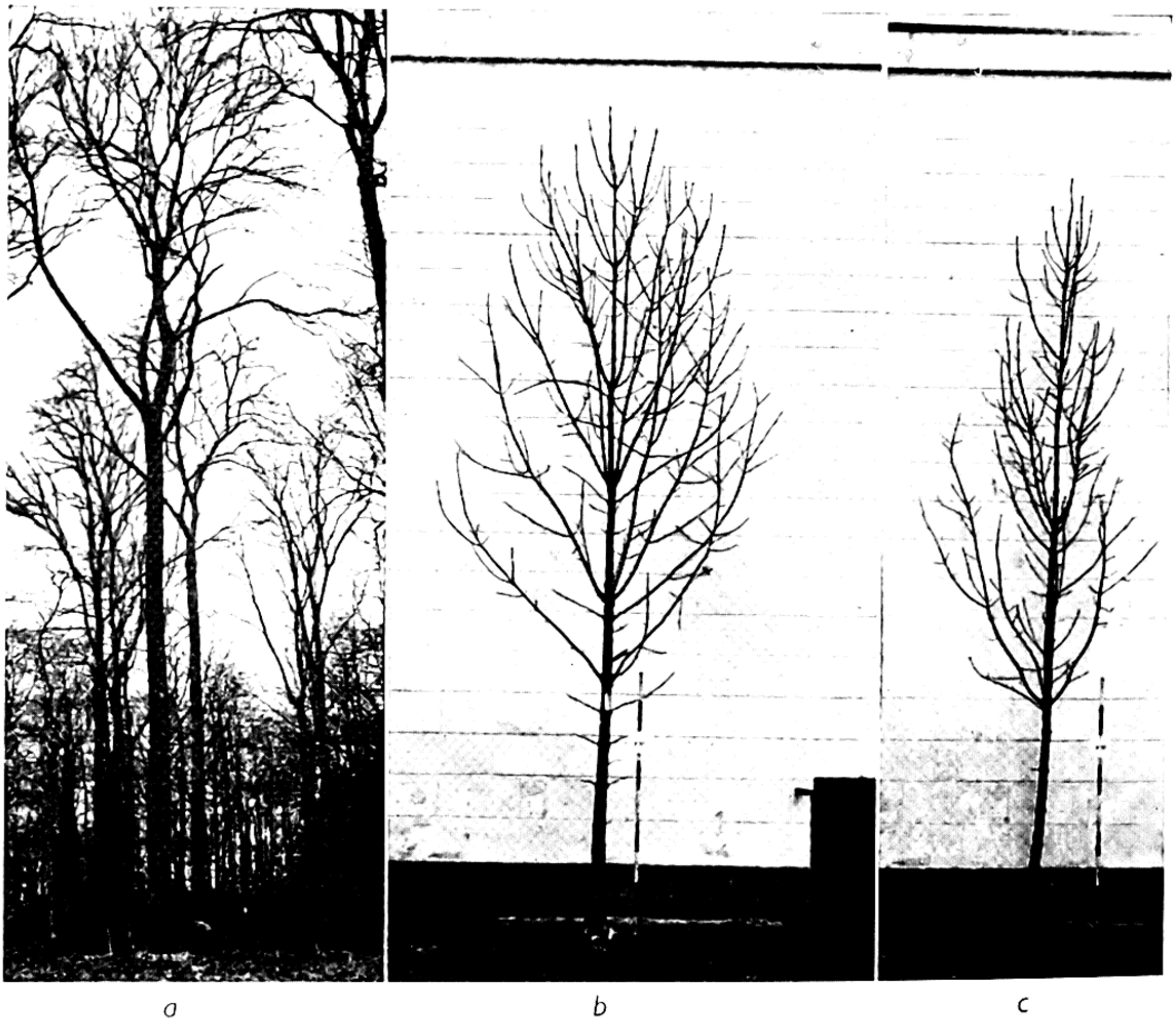


Fig. 30. *Ash* (V.282), Stenderup. (a) Original tree photographed on 14th February 1938. (b) (c) Grafts of 1938 photographed in December 1946. (*See* Fig. 23.)

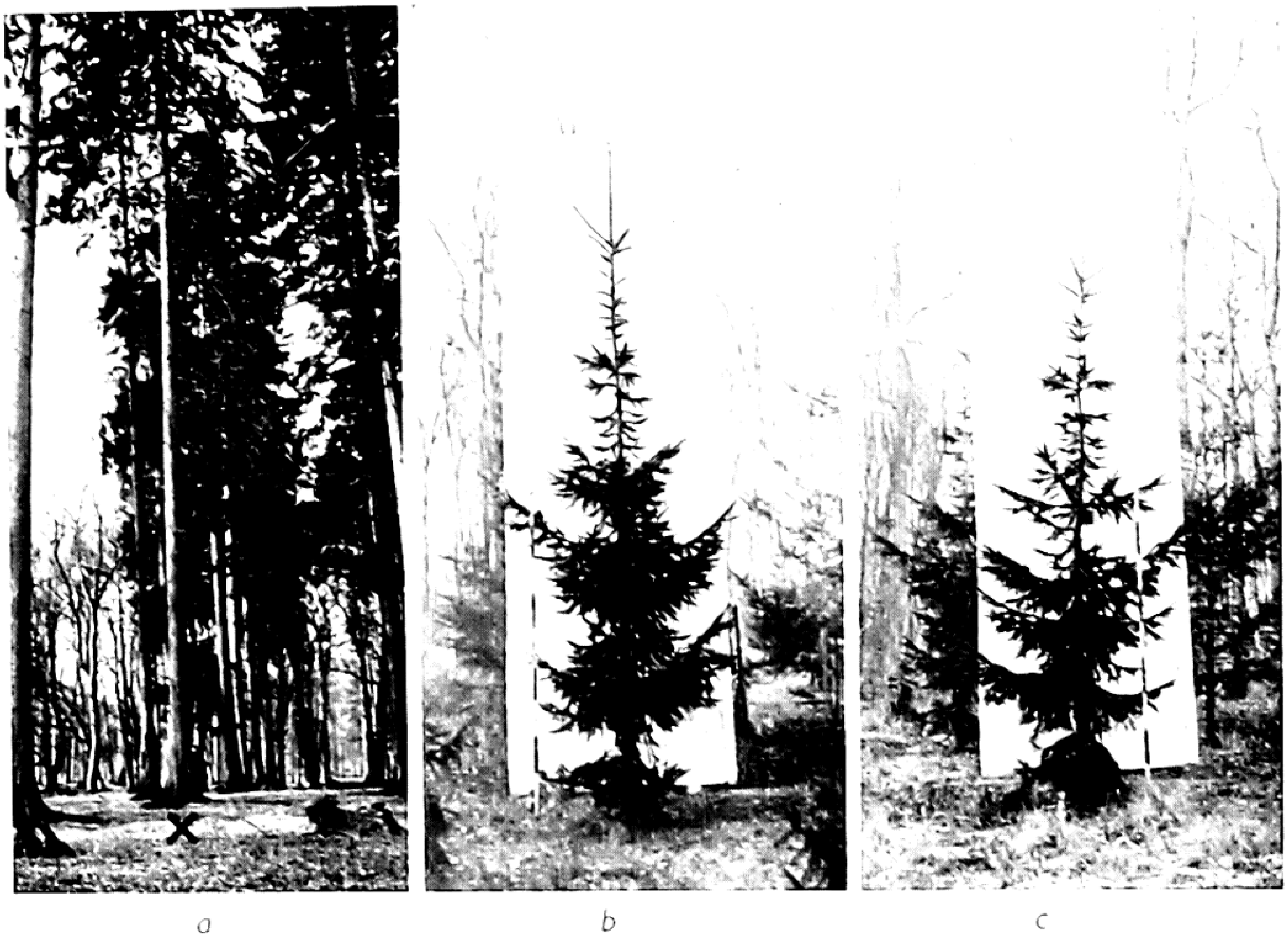


Fig. 31. *Norway spruce* (V.49). (a) Original tree photographed 25th March 1937, (b) (c) Grafts of 1936 photographed in January 1947.

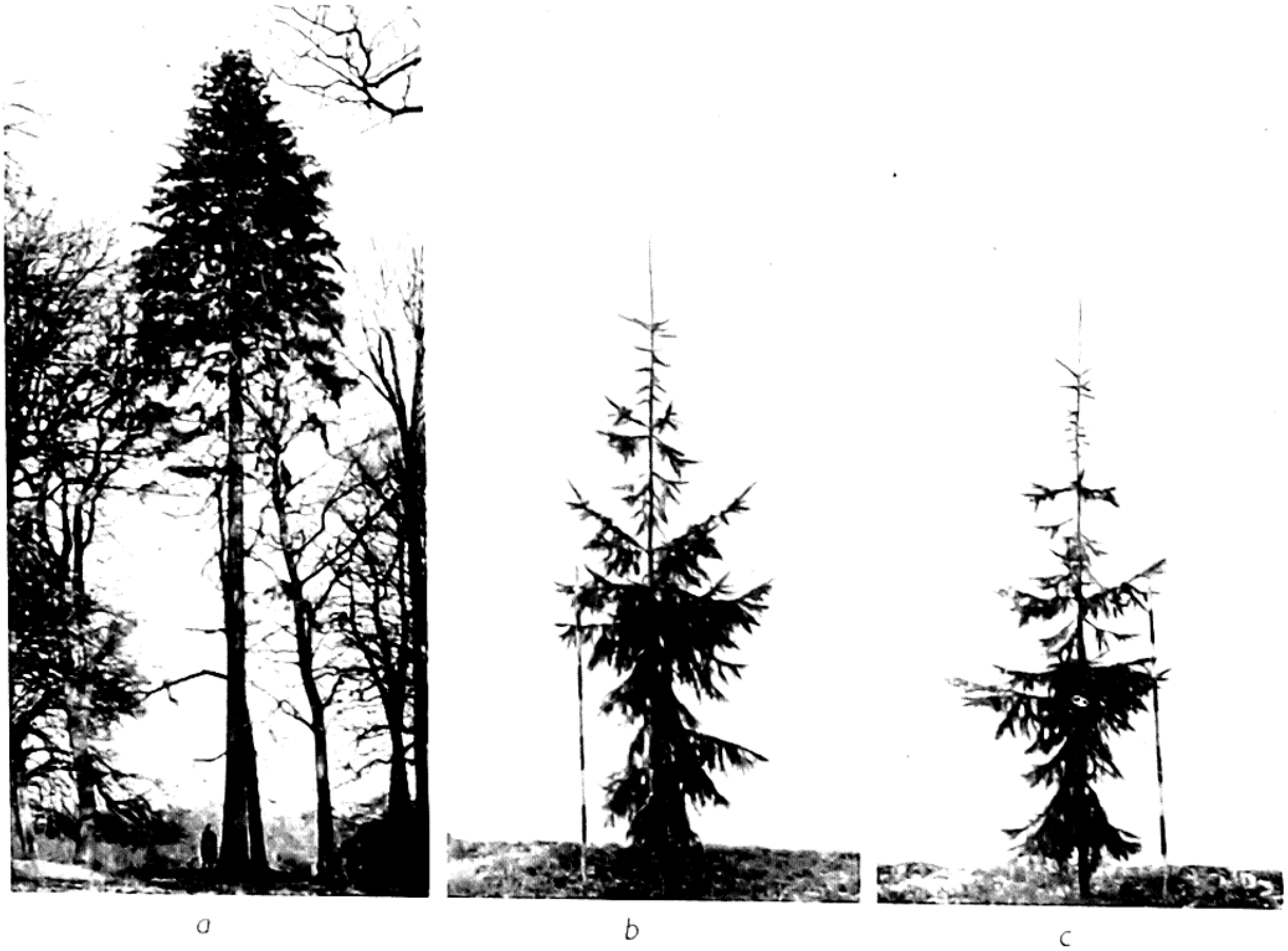


Fig. 32. *Norway spruce* (V.50) (a) Original tree photographed in 1947. (b) (c) Grafts of 1936 photographed in January 1947.

The graftings furnished grounds for thinking that the fine form of V.263 is primarily due to features determined by heredity, to its being a good genotype. There must be more doubt about V.262, in which the fine phenotype in most essentials must have been brought about by good silvicultural treatment. The special peculiarity of V.265 is its frequent formation of forks. It is by no means a good genotype, but the phenotype was believed by us when the selection was made to be amongst the best. The tree has since been felled and has furnished a valuable ship's keel. In time one always develops a better eye for the frequent forkings near the top in the free portion of the crown of the old tree. In the same way it may also be said that the extreme top of V.262 is not very good, but that might be the result of wind action due to the great height of the tree.

For ash the three clones V.4, V.25, and V.282 in which the plants were grafted in 1935 and 1936 may be used as illustrations. The material was taken from three trees on very different sites scattered over the country.

V.4 is an old, broad-crowned tree. The graftings are slow-growing and very branchy. From a forestry viewpoint they have a practically valueless form. V.25 is rather better, but also a type unsuited for economic forestry; it is, however, obviously different from the previous one. V.282 displays excellent fast-growing grafts with straight and ascending stems.

For all three clones the close resemblance between the forms of the graftings, and those of the trees from which the scions were taken, may be observed. Moreover, precise conformity was evinced between the manner of flowering of the " mother-trees " and that of the grafts produced from them.

For Norway spruce, results may be quoted for V.49 and V.50, both of which were grafted in 1936. V.49 was taken from a particularly fine tree with a slender, straight stem cleaned of branches to a considerable height in a dense stand, which, like the next tree, originated from a planting about 1765. The graftings of V.49 showed a genotype which evokes a straight and vigorous stem with good growth and with no coarse branches. Branches of the second order are stiff; there are luxuriant dark needles.

V.50 is a tree standing alone, immediately outside the stand just mentioned. It is a large tree with a heavy crown. In this case the genotype evokes a similar straight but more slender stem, with slightly weaker growth. The branches of the second order are soft and somewhat drooping. The habit of the tree is on the whole brighter and less coarse. The needles have a different colour from those in the previous example. Both are good genotypes, but they are different from one another. The tree which has been cleared of branches to some height within the stand (V.49) appears to have an innate more robust form (branching) than the isolated tree, which had had an opportunity to develop the larger crown (V.50).

For Douglas fir (*Pseudotsuga taxifolia*), reference may be made to an experiment with two trees from the natural range of the tree-species. These were selected at Wind River Forest Experiment Station in the state of Washington, where the scions were cut off in April 1946. They were flown to Denmark and grafted there a few days later.

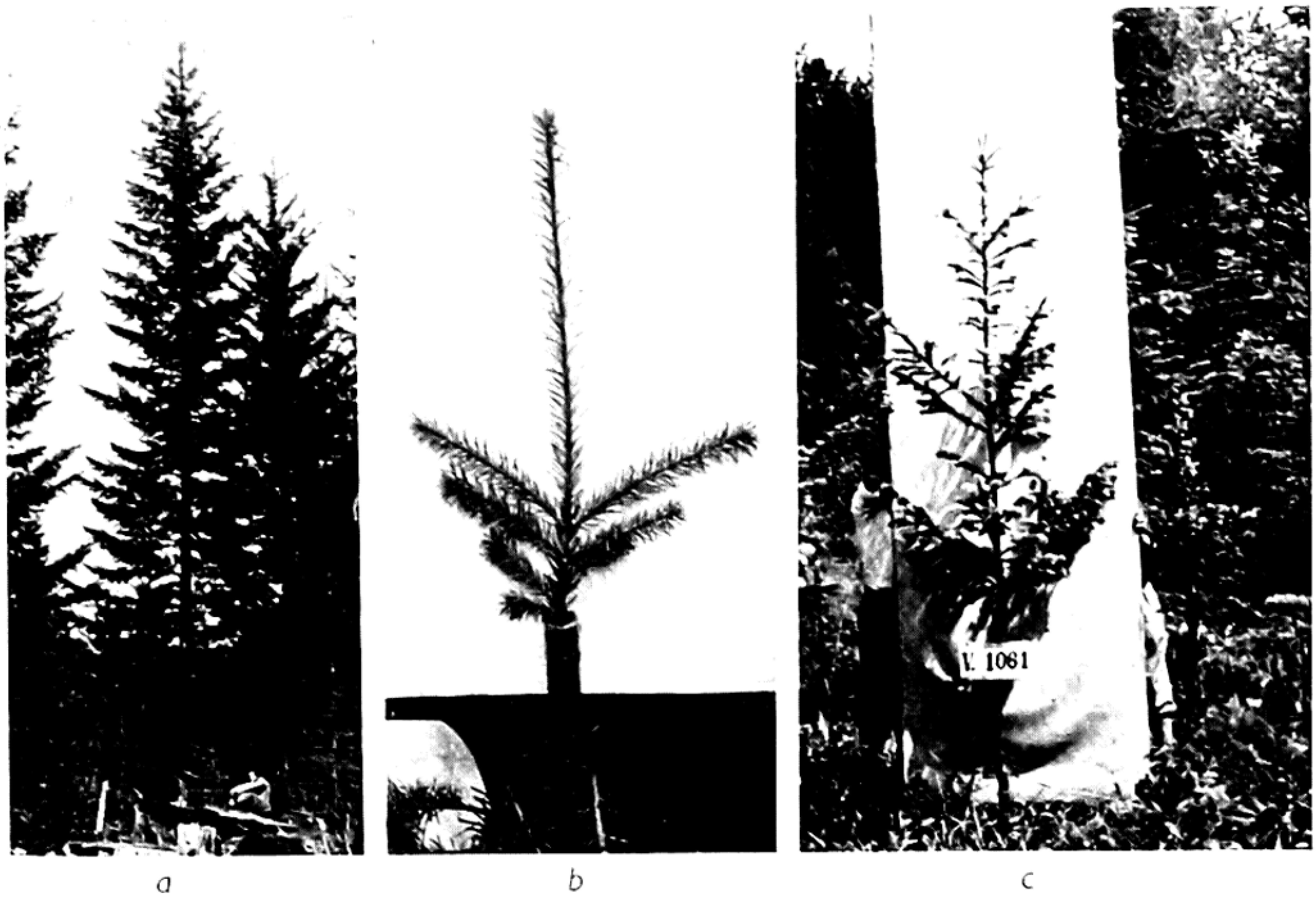


Fig. 33. *Douglas fir* (V.1061). (a) Original tree, Wind River, photographed 17th April 1946. (b) (c) Grafts in Denmark on 29th April 1946; (b) photographed on 25th September 1946 and (c) on 26th June 1950.

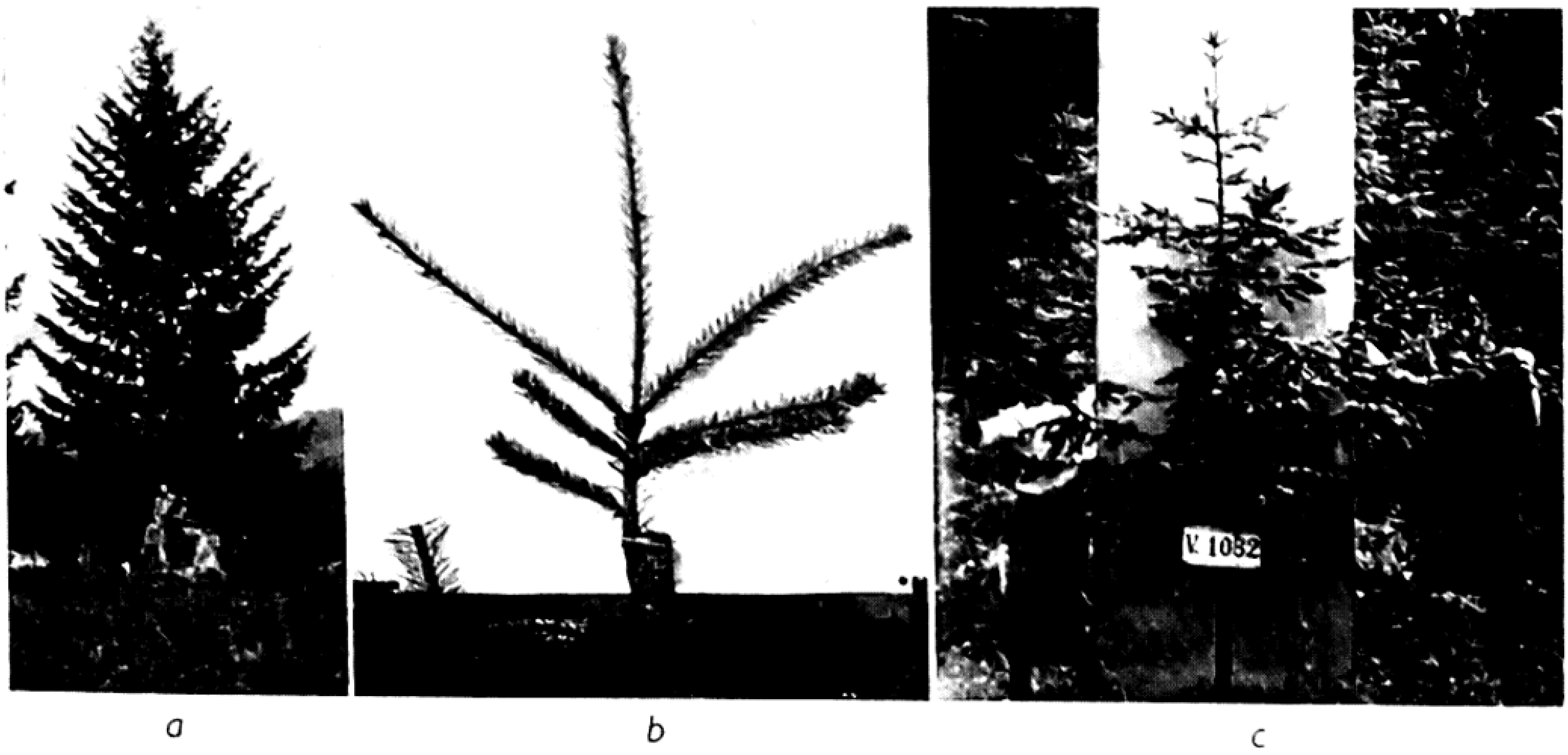


Fig. 34. *Douglas fir* (V.1062). (a) Original tree, Wind River, photographed 17th April 1946. (b) (c) Grafts in Denmark on 29th April 1946; (b) photographed on 25th September 1946 and (c) on 25th June 1950.

The two original trees are illustrated here, with their grafts in the first and fifth years. From Fig. 33 and Fig. 34 it is plainly evident that, of the two, V.1061 represents the desirable forestry type. V.1062 not only has coarse branches as a result of its isolated position, but is of a genotype which, in the open, develops particularly coarse and long branches.

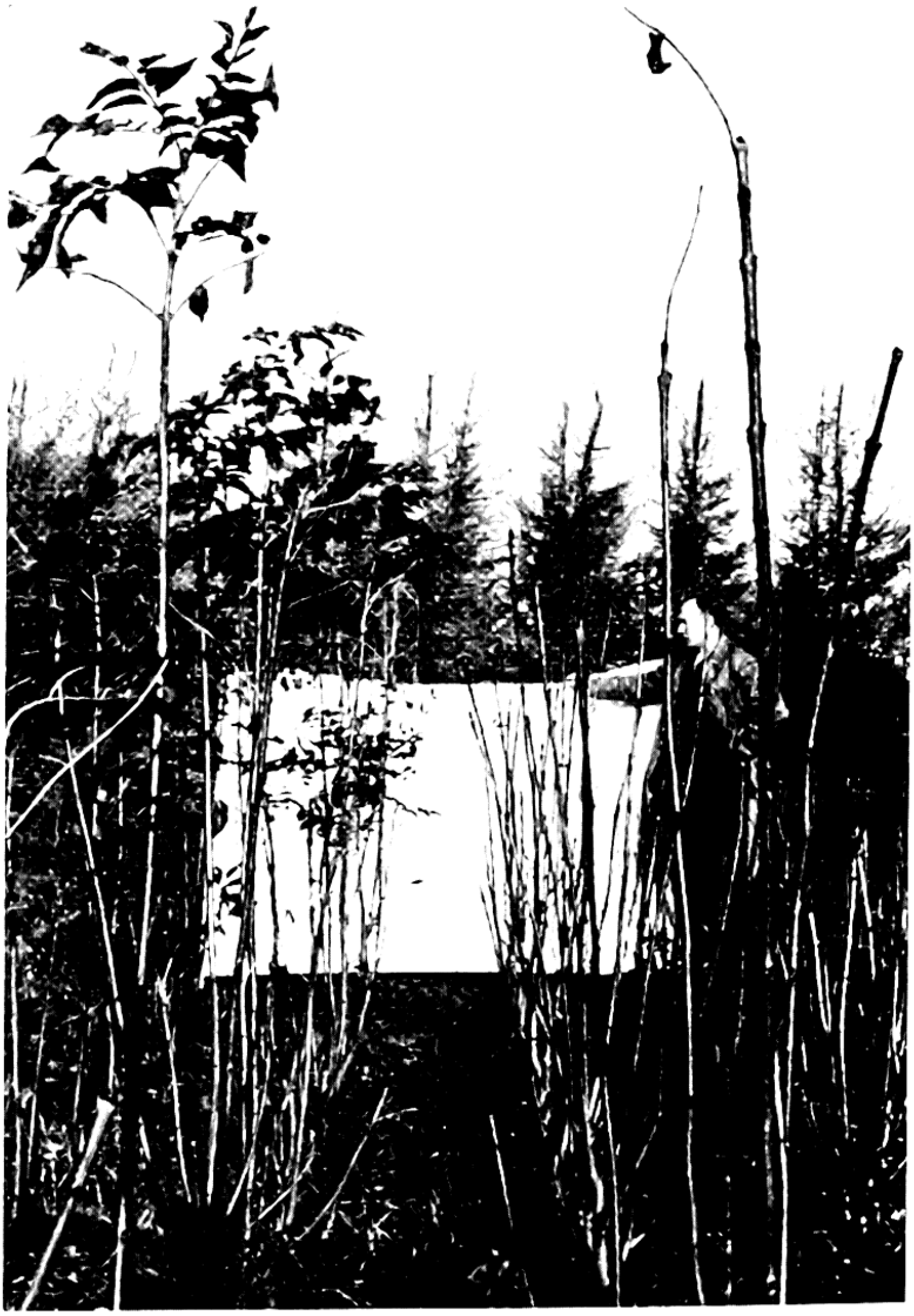


Fig. 35. *Ash.* Different times of leaf-fall in the case of two clones. V.282 to the left still has many leaves (*see* Figs. 23 and 30 regarding the same tree), whereas V.4 to the right is leafless (*see* Fig. 28 regarding the same tree).

Other experiments have been carried out with birch, larch, and pine, and they all point in the same direction. They display an obvious individual difference, which it has quickly been possible to prove with the help of tree-shows.

This is therefore an important means of *discovering the existence of different genotypes*, and for obtaining expression of the difference between them. Even if there should be some effect due to grafting, we must in any event obtain valuable relative expressions. From experience in the Arboretum here we even seem to obtain a satisfactory expression of growth-energy.

It is of great importance for forest-tree breeding to obtain reliable expression of the disparity between individuals—to obtain a means of assessing the extent to which the individual difference is genotypically determined. Tree-shows help in this, whether they are concerned with trees from the virgin forest or from the commercially managed forest. The research work to date indicates that there is a very important reciprocal difference in genotype.

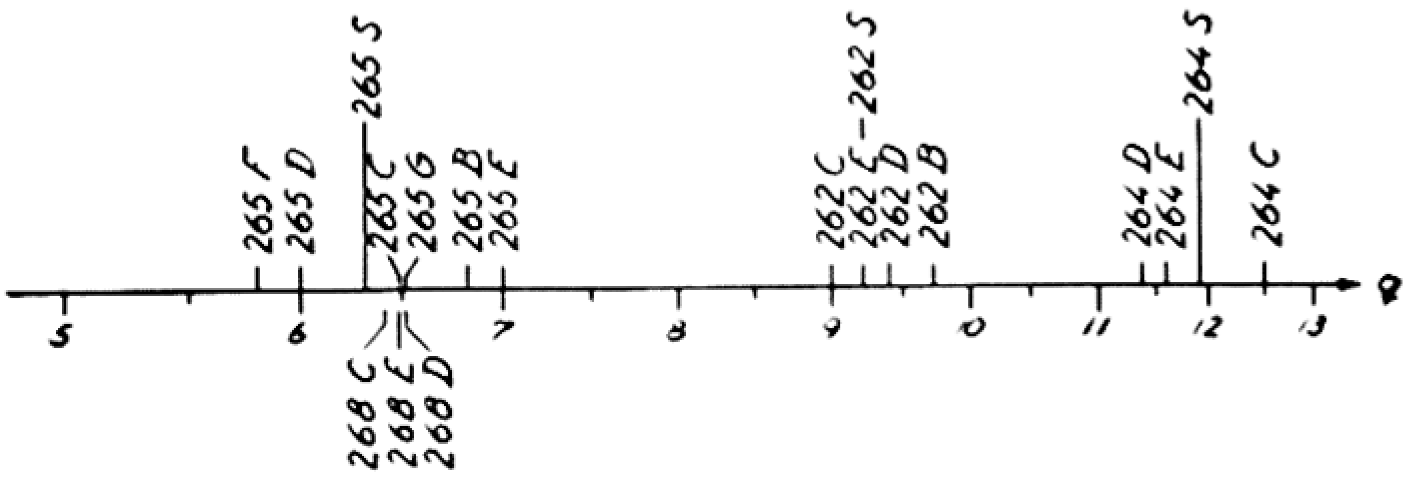


Fig. 36. *Beech*. Distribution of the value q (wood rays $\frac{\text{height}}{\text{width}}$) in 16 trees divided over 4 clones: V.262, V.264, V.265 and V.268. In addition values of q for the original trees corresponding to the first 3 clones are shown computed for branches placed high up on the trees having a thickness of 7–13 cm. (2·8–5·2 ins.)—(262S, 264S and 265S). In the fourth example the opportunity for this computation was lacking.

This encourages optimism in regard to forest-tree breeding, which, like all breeding, relies upon variation occurring in nature. It is also an inducement to keep our eyes open for possible advantages of clone formation, while at the same time going further ahead with breeding through sexual processes.

In addition to the examples already mentioned of a difference in habit and growth-vigour, there have been examples of its use for demonstrating a difference in conditions of leaf-flushing, leaf-fall, and flowering. Regarding its utilization in the plant pathological evaluation of individuals, an account will be given in a subsequent chapter.

As an example of how tree-shows can contribute to the elucidation of what may be important particulars, which may be concealed from ordinary observers, the following case concerning the wood anatomy of beech may be mentioned. The investigation was carried out on the basis of a tree-show from which the samples of beech in question were taken. The work was performed by E. TELLERUP and M. SCHAFFALITZKY DE MUCKADELL and published from the Arboretum here. (E. TELLERUP and M. SCHAFFALITZKY DE MUCKADELL: " Individual Differences in the Shape of Wood Rays in *Fagus sylvatica L.*," *Royal Veterinary and Agricultural College, Copenhagen, Yearbook*, 1953, pp. 147–157.)

Prior to the investigation nothing was known by us of any different structure of the wood in individuals of the European beech. From the direct examination of wood samples the impression obtained was even one of rather strict homogeneity. That was why it was interesting to find out whether from closer investigation it might be possible to prove that there are anatomical differences in the timber of the clones used.

M. SCHAFFALITZKY DE MUCKADELL conducts our research work into the improvement of the Danish beech, and E. TELLERUP is employed in the detective force, from which he is very closely acquainted with the importance of detail. This is mentioned as an example of the importance of co-operation, which is very important in so new a subject as forest genetics.

They were on the point of giving up the task, when TELLERUP found a difference in the medullary rays of the different clones. In the tangential section the height and width of the medullary rays were measured, and the ratio between them was expressed by a constant q—the value of q in 16 trees distributed over clones V.262, V.264, V.265, and V.268 is shown in Fig. 36.

As an example of the clones which differ most, the tangential sections of V.264 and V.268 are shown in Fig. 37. The pictures were typical of the respective clones in several grafted individuals, as well as in the branches and in the stems of the original trees. It was thus found to be an individual peculiarity of the clones in question.

When such differences can be proved to exist in the anatomy of the wood, the obvious thing is to go further and find out whether the proved differences bring about a different value in the technical use of the timber, or whether such a difference would perhaps result in a varying resistance to fungous attack. Similarly, the example will stimulate investigations into the relative thickness of heart-wood to sap-wood in other species. Timber is, however, the product sought after by the efforts of the forester. It will therefore be of value to employ tree-shows in the selection of individuals with the proper anatomical structure for future use in breeding. That may be just as important as to get individuals with the right form, growth-energy, resistance to frost, etc.

While we regard all these qualities as valuable in our future breeding work, we can again consider ourselves fortunate in dealing with long-lived individuals, which we can reproduce vegetatively. This furnishes us with the means "*of preserving in the future* our most luxuriant individuals from a forestry point of view, thus solving a problem which has been tackled in vain by libraries, archives, and museums, and which is of the utmost importance

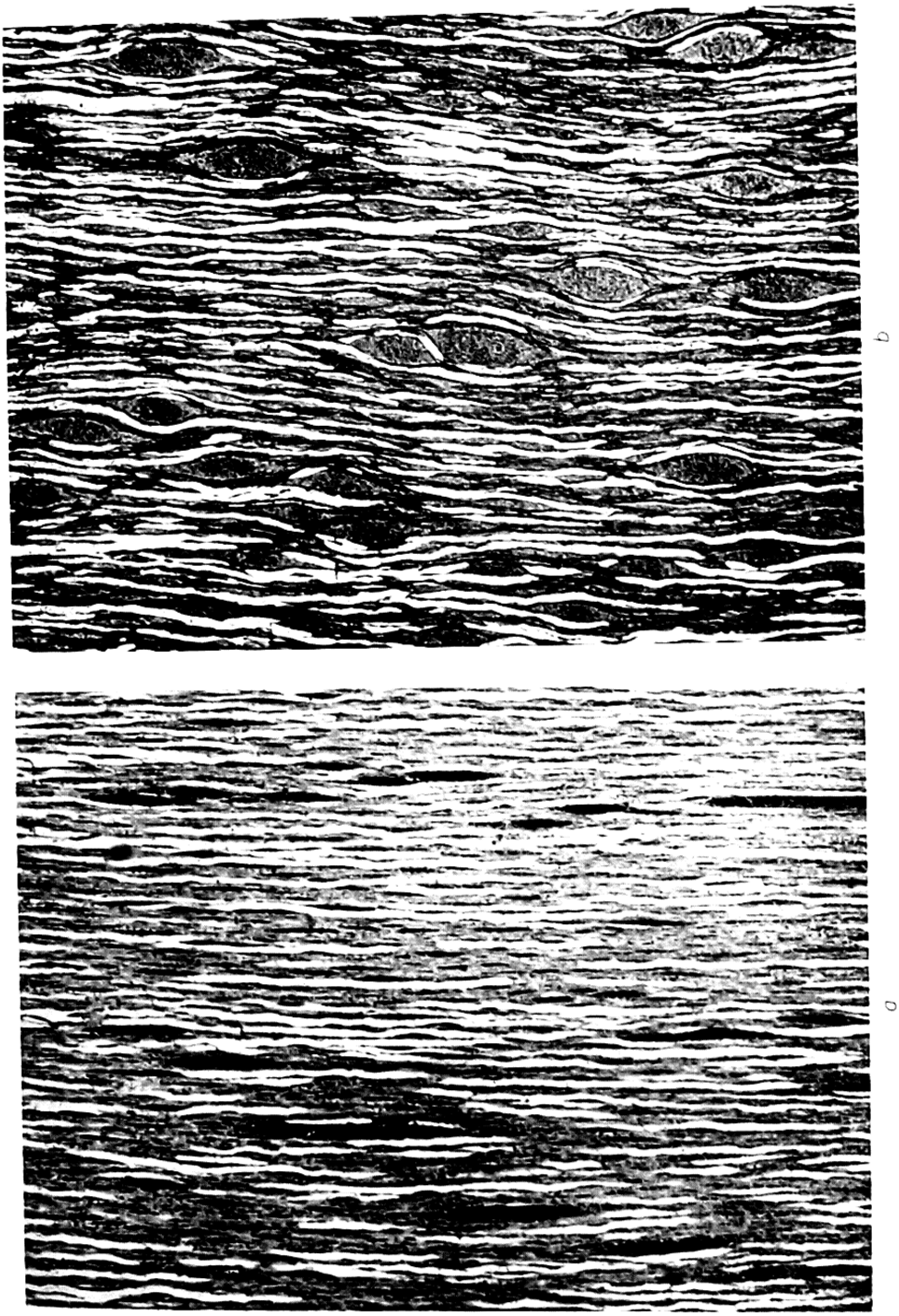


Fig. 37. *Beech.* Tangential sections of wood in two clones with clearly differently formed wood rays. (a) V.264, sample *A* with q equal to 13·0. (b) V.268, sample *A* with q equal to 4·6.

to forestry, as a basis for improving our forest trees " (*Forest Tree Breeding*, 1934, p. 111). Moreover, if we have the individuals arranged in tree-shows in association with our arboreta or forest research stations, they can be subjected to *continuous observation and examination.*

Grafts are parts of the original trees, so that they can also be kept as grafts in flower-pots for experiment in greenhouses and cool laboratories, or planted out in widely scattered localities in order to test their reaction to various climates. In this way it should be possible to find some guidance for dividing the trees into " climatic races " (ecotypes) and to contribute to solving the question of the extent of the climatic regions which the individual types may be presumed to cover. It will be very different from those experiments in which the work is done with seeds, and one can make a choice for examination only from what has been sown out and has chanced to survive.

We have thus advanced to the point of considering the problem of *examining the individual genotype under different phenotypic influences*—or of one clone in different places. This is an important task, which may contribute, for example, to a more detailed investigation of the importance of the planting distance for cleaning up the stem and for growth. It may even be taken further to deal with the question of the correct method of thinning, with investigations into the use of shade, shelter, and so on.

By choosing a number of " type-trees " of various species, their employment in clones may be used for registering the climate of different localities through such selected individuals (clones). They would act as a kind of " live meteorological station ", which would certainly prove of value, when we consider how small a part of the combined climatic conditions the meteorological factors which are now measured comprise.

If we glance back to what was said about the evaluation of the genotype, it would appear that there are also features in it which can be interpreted as a compliment to the forester's handling of the stands. Attention should be drawn to this matter, although it must be put forward with certain reservations because no comprehensive data are yet available.

When such fine trees as two of the beeches referred to (V.262 and V.265, Figs. 25 and 27) have turned out to be not very satisfactory genotypes as regards growth-form, whereas at the same time the original trees have risen to be amongst the best in the forest, we have evidence that silvicultural treatment with a dense stocking and careful thinning has attained its object of improving the form. The fact that the good genotypes are most often to be found among the finest trees in the forest is a rather different matter. Lastly, we must not forget that we earn increment by working with good populations, which do not need to be " trained " so intensively. They may be grown in a more isolated position and make use of more light in production at an earlier date, while at the same time becoming well shaped.

While silvicultural tending contributes to making the trees in the stand more attractive (better phenotypes), it also means that it brings about a phenotypic obliteration of the genotype of the individual trees. Perhaps, therefore, we should not count too much upon a genetical " improvement " through thinnings of stands which are treated silviculturally. It must therefore be recommended to pay just as much attention to the outstanding trees in the untouched forest and where the species has had to put up with specially harsh external conditions, as where we can choose individuals in silviculturally managed forests. The latter may have displayed special tractability to training.

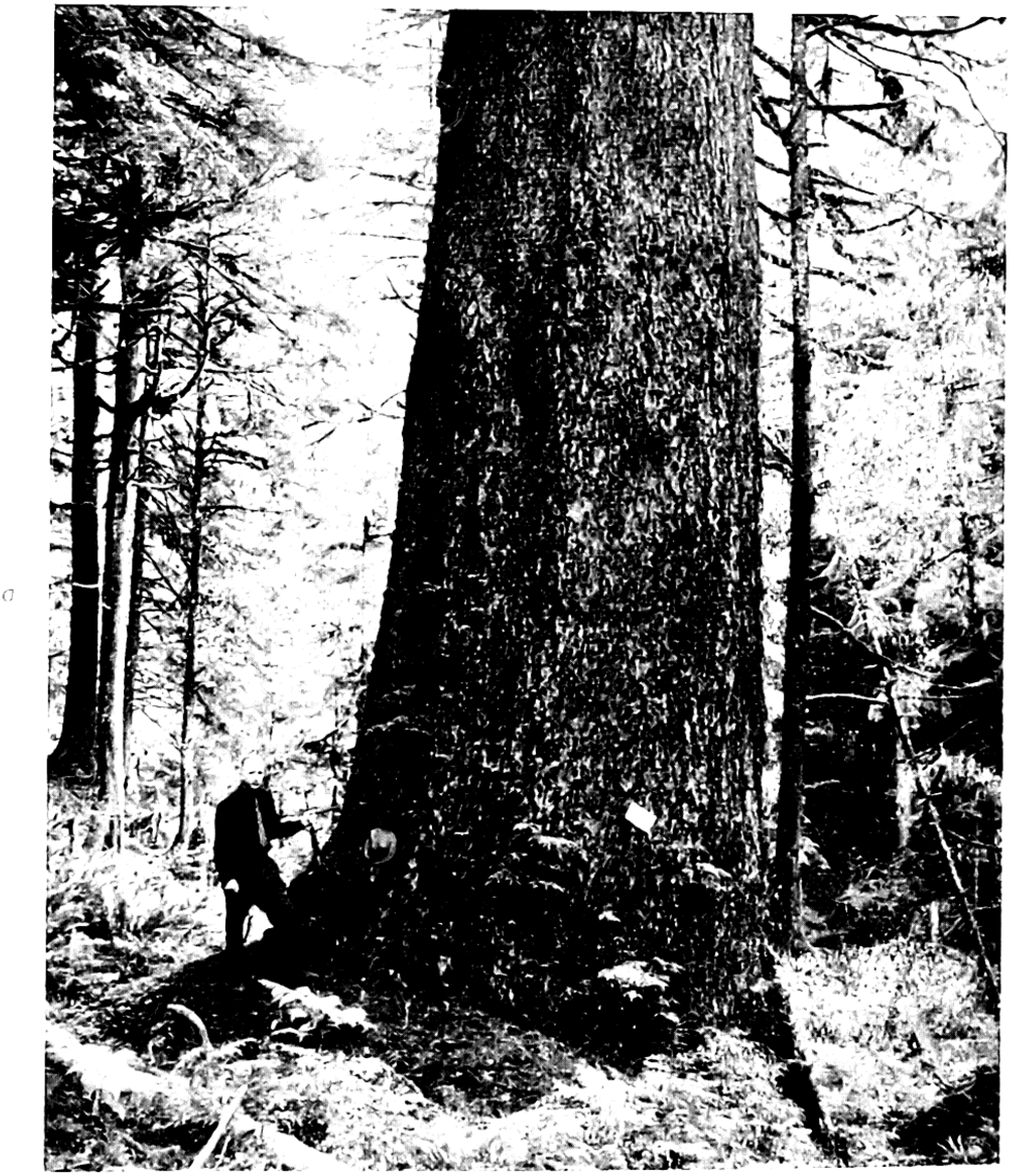
In choosing for breeding, a great deal of attention must be paid to the fact that it is not merely a question of demonstrating a visible difference in genotype by means of a single tree-show. That is only one step on the way. Different genotypes have *different capacities for adapting themselves* to altered conditions. It is important to remember that such difference in adaptability is determined genetically. It is of particular importance in forestry. The long rotations, the dense stocking of the trees, and the gradual thinning out make it possible to make use of individuals with valuable inherent tendencies in respect of adaptability. It is therefore important to work with trials of the individual genotypes under different external influences. The individual genotype must be demonstrated in different phenotypes.

When we work in Denmark on the breeding of Douglas fir and have selected for that a considerable number of trees both from Danish stands and from the finest artificial stands in neighbouring countries, we also include, however, a tree like " Oregon's largest Douglas fir ".

This tree stands northwest of Portland, not far from the Pacific Ocean, on CROWN ZELLERBACH's property. It is a giant with a diameter at breast-height of about 4·5 m. ($42\frac{1}{4}$ ins. Q.G.), and it is still a vigorous tree, where the top has snapped off at about 63 m. (206 ft.) above the ground. The tree is standing in a geographical region which might well be expected to provide us with something of value. Perhaps it contains those valuable tendencies which induce a specially vigorous growth. It would be surprising if the giants, even if they only represent crude force, did not also contain something good. I am of the opinion, indeed, that " loss of growth-energy " may be one of the most dangerous irrelevancies in breeding.

It is in any event worth while trying to test out such a tree. By including it in our vegetative propagation as graftings in our tree-show we shall quickly obtain an answer.

We should preserve in tree-shows such giants and other " pioneers " which have shown exceptional development, and we ourselves should also keep " pioneering ", which should make their further use possible.



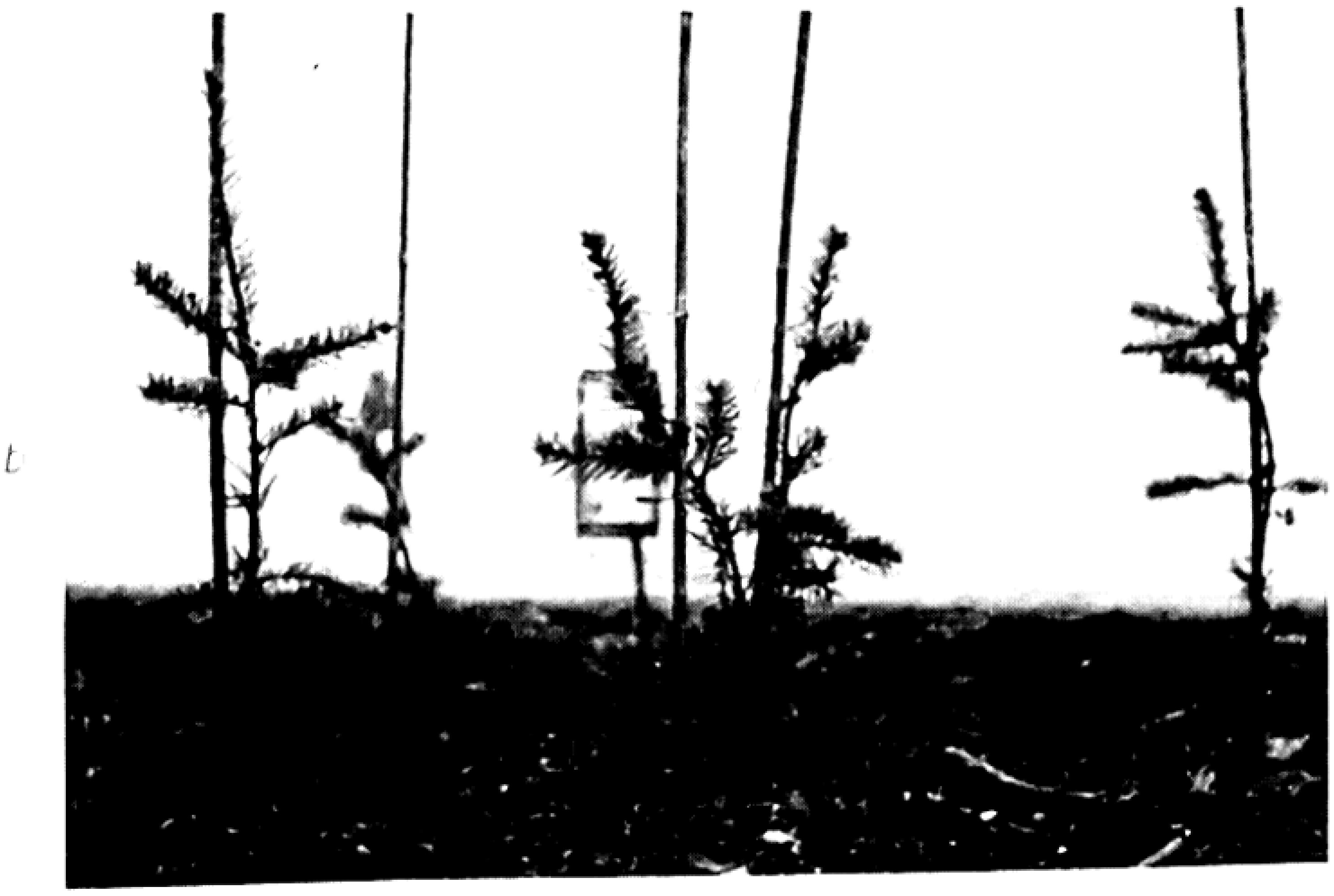


Fig. 38. *Douglas fir.* (a) "Oregon's largest Douglas fir". West of Portland. Diameter at breast-height about 4·5 m. (42¼ ins. Q.G.). The top has snapped off at about 63 m. (206 ft.) from the ground. Photographed in July 1946.

(b) Grafts, two years old from this tree; V.1861/53 in the Arboretum at Hørsholm, photographed 8th Jan. 1955.

We must realise, however, that by finding these good genotypes we have not yet solved the problem of good trees for breeding, but we have on the other hand made an important step forward.

Breeding must also have some connection with progeny trials resulting from free pollination, and we must make use of those opportunities which vegetative reproduction gives us of getting small early-flowering examples of the same clones—like those studied in tree-shows—for use in controlled pollinations. (Cf. Fig. 23.) Whenever it is easy to obtain many readily available female flowers to work with, it is, moreover, possible to do the mutual pollination systematically in such a manner that for a series of selected individuals a common father can be used, for example. In that way a valuable basis can be found for comparisons and progress by another route in the analysis of the value of treees as breeding trees. See " polycross ", p. 15.

For all the tree-species, which will later be subjected to attention through a use of repeated thinnings, we have the consolation, as the work progresses, that there is not, as in other cases and as, for example, with most agricultural crops, any over-riding demands made in respect of uniformity. The primary problem will be to remove the poorest individuals from the progeny, and to make sure of getting a considerable number of the very best represented.

It is often said that, in order to acquire sufficient knowledge of a crop—in our case the mature forest—there must be an opportunity of following the development from seed-time to harvest, or, as it is often expressed, " from the cradle to the grave ". That is quite correct, but it takes such a long time in forestry. One man cannot always do it; his work must be followed up by the next generation and perhaps by the next again. We would lose heart if we thought of that as being the only way. I would like to change this round, and so express it that in the forest we have a better chance to follow the tree from " the grave to the cradle ". That is what we are doing when we employ tree-shows. We pick out our finest phenotypes among the old trees, which may be said to be standing on the edge of the grave in the mature stand, and graft them into tree-shows, which may to some extent be regarded as " cradles ". That provides us with the opportunity for observations which may explain how the individual was able to grow up to be one of the finest trees in the forest. Although that does not give the complete answer, it is nevertheless a step on the path towards it. It is one of the " short-cuts ", which we must utilize, and which the long-lived individuals render possible.

When estimating the genotype in this way attention should be paid to the existence of development stages in forest trees. (See M. SCHAFFALITZKY DE MUCKADELL: " Juvenile Stages in Woody Plants," *Physiologia Plantarum*, 1954, Vol. 7, pp. 782–796.)

Further, we must not under-value the significance of the fact that we can go back when we like to our depots or tree-shows in order to look for comparisons or fetch living material from them with known qualities.

The study of our vegetatively reproduced trees in tree-shows, and of how we otherwise use them, makes it possible for us to delve deeper and deeper into *analyses* of the selected individuals. We can thus to a great extent relieve our provenance trials and other progeny trials—which to too great an extent lay up work for the future and postpone the answer. We must rather work away with what we have been given in our forests. It is probably not any dearer than the expenditure which we otherwise expect in the future. It is even possible that we may happen to be performing a task which will later prove to be highly profitable.

Aided by vegetative propagations we can have the means at hand for analysing our already existing material, and we can take a long step forward towards the objective of producing the seed we desire from them. Similarly, engineers and architects must first know their materials in every detail before building magnificent bridges or other structures from them.

Forest-tree breeding will break away in many ways from the methods of procedure adopted in agriculture and horticulture. We must be prepared to break our own trail. I myself believe that forest-tree breeding will in future largely come to resemble chemical analysis and the research work of the engineer—and by such methods important results have indeed been achieved.

CHAPTER VIII

BREEDING AND DISEASES

TREE-SHOWS can help the forest-tree breeder to obtain in a few years an insight into the individual variation within a species. The results may be so pronounced, and appear so reliable, that the reaction of certain individuals to diseases in particular may encourage the immediate widespread use of the promising individuals in vegetative reproduction. This use of clones is commonly familiar in agriculture and horticulture, but with regard to forestry special conditions hold and involve a closer consideration of their use in the future.

In this connection it must again be recalled that trees are long-lived individuals, and we must also bear in mind, in respect of a forest stand, the peculiar method of harvesting the individual trees at different times. The important yield falls due at the final felling of the stand, but before that time in an intensively managed forest an equally large volume of timber has often been realized as the yield from repeated thinnings.

On account of the long rotation, plant-breeding in forestry must to a great extent be characterized by efforts to ensure resistance of the progeny to disease. We are less bound to bother about a demand for uniformity. We can harvest the individual tree in a thinning or let it stand until the final felling, whereas the farmer must take in his crop all at one time. Should the farmer, on the other hand, find from experience that a " strain " is attacked by disease, he can change over to a new strain from one year to another. The forester cannot do so. He would suffer heavy loss if he were compelled to fell a stand before it had reached maturity.

We can therefore lay down a provisional objective for forest-tree breeding in all cases, namely, that it should strive to get the stands to become more uniform by freeing them for the most part of the poor individuals. This applies both to resistance against disease and to growth-energy and form.

The form of the tree readily strikes the eye, and it is natural that we should have special regard for it; but it must not be forgotten that we certainly have a very good opportunity to improve the form by appropriate ways of working, whereas it is a different matter with growth-energy. The result of the latter may be related to resistance, but we have an opportunity to appraise all three factors, as well as other individual attributes, through our tree-shows.

From an evaluation of a series of individuals in a tree-show one may become enthusiastic about a single individual. It may appear to have all the desirable qualities, and one may be tempted to make further use of it in afforestation by use of vegetative methods. The use of clones in this way may be so inviting, that in the intensively managed forest it may appear to be the only reasonable procedure. This happens in many countries in respect of the use of poplar clones, and in Japan, where they use clones of *Cryptomeria japonica* (Fig. 17a).

Whilst putting on record the existence of such a use of clones of poplar and *Cryptomeria*, they must of course rather be referred to as the rare exceptions. On the whole it must be a gamble to use a clone, although the prize from a lucky hit may be so great that people are willing to go to considerable expense to establish plantations and to run the risk of failure. In general a warning must be given about making too narrow a choice, so long as we still have only a limited knowledge of the qualities of our trees.

In the case of the narrowest choice of all, with one clone, we can from the start obtain for ourselves the greatest possible advantages, since for our starting-point we are choosing a thoroughly tested individual. We must not only have tested its development in comparison with other clones under the same conditions, but we must also have tested it under different external conditions. It can, however, only be subjected to those phenotypic effects we know to-day. A different situation may arise with the appearance of new unknown types of fungi, just as is known to be the case in agriculture and horticulture. (H. VAN VLOTEN: " Is Enrichment of the Myco-flora Possible? (in relation to poplar rust)," *Tijdschrift over Plantenziekten*, 1944, p. 59; and "Crossing Experiments with Strains of *Melampsora larici-populina* Klebahn," *ibid.*, 1949, pp. 197–209.)

In the other land-uses it has been possible to take greater risks in the use of clones, because there is an opportunity to change over quickly to another clone. Moreover, with them, extensive use can be made of chemical means in combating diseases. It is not ruled out that spraying may find wider application in forestry, and in particular become important in meeting an acute attack which is favoured for the time being by external factors.

The effect of a chemical liquid may be so strong that it completely eliminates the danger, but it may also have so strong a " one-way " effect on the harmful organism (fungus or insect) that, in the same manner as in our breeding, it forces development in a certain direction—which is not, however, the one desired. It is to be hoped that we shall continue to find new opportunities for dealing with pests which are likely to be intensified or specialized. That will always involve an economic burden, however, and possibly a danger, which can only be overcome when there happens to be at the same time a chance of economic gain.

An obvious example of the interplay between the use of clone and population occurs in the cultivation of poplar and aspen. Something similar also holds for larch and thuja at the stage at which we now find ourselves in Danish forest-tree breeding. The use of clones of poplar, with their advantages and disadvantages, is generally known. In Denmark one of the greatest dangers is an attack of rust (*Melampsora*), which has shown itself to be very destructive on clones of poplar, although they have been promising for several years.

Our European *Populus tremula* is seriously attacked by rust, whereas the American species *P. tremuloides* has shown itself to be extremely resistant in this country. When the Swedes, and ourselves immediately after them, had obtained very promising hybrids by crossing *P. tremula* and *P. tremuloides*, it was tempting, just as it was with the poplars, to go in for selection and cultivation of clones, although in this case vegetative reproduction is rather more difficult than with the true poplars. An individual variation, which is often considerable in an otherwise wholly promising progeny, might be an additional incentive to experiment with cultivation in clones. The reasons why we in this country threw ourselves promptly into the commercial use of seedlings are as follows.

Although we can produce clones of the most promising hybrid plants, and may possibly in so doing achieve something outstanding, we have nevertheless for the time being thought it best to disperse the hybrid in populations. A population is in itself promising material, and it is obtained without the individuals being mutually identical, which might become catastrophic if there should arise a type of *Melampsora* which was specially equipped to attack a selected clone cultivated on a large scale.

In Denmark we have therefore felt that, at least for the time being, we shall best ensure an increased output by working with a production of seedlings repeated every year. The seed is produced in greenhouses by artificial fertilization, so that there is control over the trees used for breeding. The latter are, moreover, not always the same and they are combined in different ways, so that a highly productive progeny is secured, which at the same time presents considerable mutual variation. It can therefore be employed with great assurance, and an advantage is also derived from the fact that under the conditions typical of forestry only a small number of the transplanted plants attain to large size, where the increase in value is the only thing that seriously matters.

That is the upshot of a certain caution, and caution may, as we know, be carried too far. What has been stated must in no way, therefore, be taken to imply that we cannot proceed more boldly. With the tendency which prevails to allow ourselves to be lured on by the brilliant results in other land-uses, it is nevertheless necessary to think twice. Many and very promising clones have turned out failures, as we know from both farming and gardening, and besides, clones are not altogether easy to handle in stands, which have to be subjected to thinning. Great uniformity has its weak points from a social point of view.

Whether at present we venture to make use of single individuals for dispersal by clones, or we choose a greater or lesser number of individuals for use in seed-gardens, it must be on condition that we know as much as possible about them from trials in tree-shows. We must not merely rely upon the phenotype, upon how the trees look in the forest, often scattered over wide distances and grown under very different conditions. In this connection we should in the first place stress the importance of a knowledge of the reaction of the individual to diseases.

Some diseases may be utterly devastating, so that, at least over limited areas, one becomes convinced that it is quite impossible to fight against them. In the majority of cases, however, one gets a clear impression that the plants are attacked either to a greater or lesser extent.

Lophodermium pinastri may occur as a serious attack upon young plants of Scots pine. In *Der Züchter* of 1929, F. v. LOCHOW reports research work which proved that the attack is to some extent due to heredity. This appeared from experiments with progeny from individual trees after free pollination. Such a promising result indicates that considerable progress may be made with further use of artificial pollination and vegetative propagation.

It would be remarkable if forestry could not, by breeding, achieve considerable progress in the struggle against diseases. Forest trees, just like other living organisms, must be presumed to contain a great individual variation in respect of their capacity to resist diseases. The task of the forester is to ensure the growth of the trees throughout a long life. We must, therefore, first of all, be able to ensure them against attacks of disease, so that breeding for resistance to disease is of special importance in forestry.

A tree-show can help us in a surprising way to an estimation of the qualities of the clones used in it. After a simple comparison of clones under identical conditions we can go on to making a trial of the individual clones. This can be done by planting them out on different areas, especially by engrafting them upon trees in a stand attacked throughout, where one can be sure that the disease is on the spot and living under conditions favourable to it—or an artificial test of them can be made at research stations, where equipment exists suitable for the purpose. We would thereby to some extent, however small, approach the analysis of the chemist and would have material available from which it would later be possible to select (by clones) or produce (through seed-gardens) what was wanted.

The largest tree in Denmark is an *Abies alba*, the central European silver fir. The height of the tree is a good 46 m. (150 ft.), the diameter at breast-height is 150 cm. (62 ins.), and it contains close on 30 $m.^3$ (810 H. ft.*) and it is 175 years of age. Along with other specimens of the same age the crown rises high above the surrounding beech forest and stands as a magnificent remnant of the first forest planting in this country of this valuable tree-species. It is not possible to-day to obtain sufficiently reliable historical data to form an opinion of how these trees grew in their youth. It would otherwise be very interesting, for this tree-species has nowadays very widespread popularity in Danish forestry, but at the same time also suffers severely from attack by *Chermes piceae*. How is it that these old trees have overcome the attack, or has there been a selection of sufficiently resistant trees? Or is it perhaps that they would have succumbed to the disease if they had stood under less favourable conditions? At an age of forty to fifty years an attack by *Chermes* is not considered in this country to be dangerous for *Abies alba*. The trees were introduced as seed and not as plants; thus it may be that *Chermes piceae* was not found in this country when the old trees were living through their dangerous age.

In a case such as the preceding one, it must be of value to forest-tree breeding and to forest zoology to be able to work with tree-shows which have arisen by grafting from individual trees. One could take the line of establishing seed-gardens with seedlings from the old trees, which would most probably, however, have been pollinated from other intrusive silver firs. It might be rather better to do it with seed-gardens of graftings, which are located for mutual pollination on a site which is fairly isolated against outside pollination. At the same time it would be useful to have them arranged in tree-shows, so that a more intensive evaluation of them can be carried out. They cannot be taken back for a comparison with their earliest youth—but they would, in a sense, however, be carried back " into the cradle ".

After having succeeded in raising a sufficiently strong and uniform material reproduced vegetatively, one can go a step further and subject the individual clones to different external effects, and of course observe those which are now prevalent in our forests with an extraordinary prevalence of *Chermes piceae*. In this more intensive test, consideration must also be given to the fact that it is not only the external conditions like rainfall, soil-type, and frost which determine the plant's greater or less power of resistance. It also seems as if the tree in the dense uniform stand is in a worse position than when the plants grow out in the open.

By using graftings, in which the aerial part at least is identical from a genetical viewpoint, much information may be furnished about the value for future use of the single individuals. It is possible that a simple trial in tree-shows will direct attention to single specimens among them that are specially promising—and, what is just as important, will allow the most unreliable to be weeded out from time to time before time and money are spent on them, or before they have lured us on a wild goose chase.

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* H. ft. = hoppus foot = 1·273 cubic feet.

The Arboretum has carried out a small pioneer experiment with clones of old material from two of the old *Abies alba* mentioned, and from a third tree in a similar stand. This was grafted in 1943 and so far has developed freely and satisfactorily, but nothing more can as yet be deduced from it.

Now *Abies* is not at all easy to work with, as cuttings are difficult, and grafts demand specially careful attention and a rather long time to develop into plants of normal form. It is an easy matter, however, with larch, Douglas fir, and thuja, and some examples from them should be mentioned. We have worked longest with larch; Douglas fir is specially interesting owing to its two forms, " blue " and " green ", each having its own enemies; and thuja is easily distributed in clones by making use of cuttings. Conditions are thus rather different in the three trees, which makes them well suited as examples.

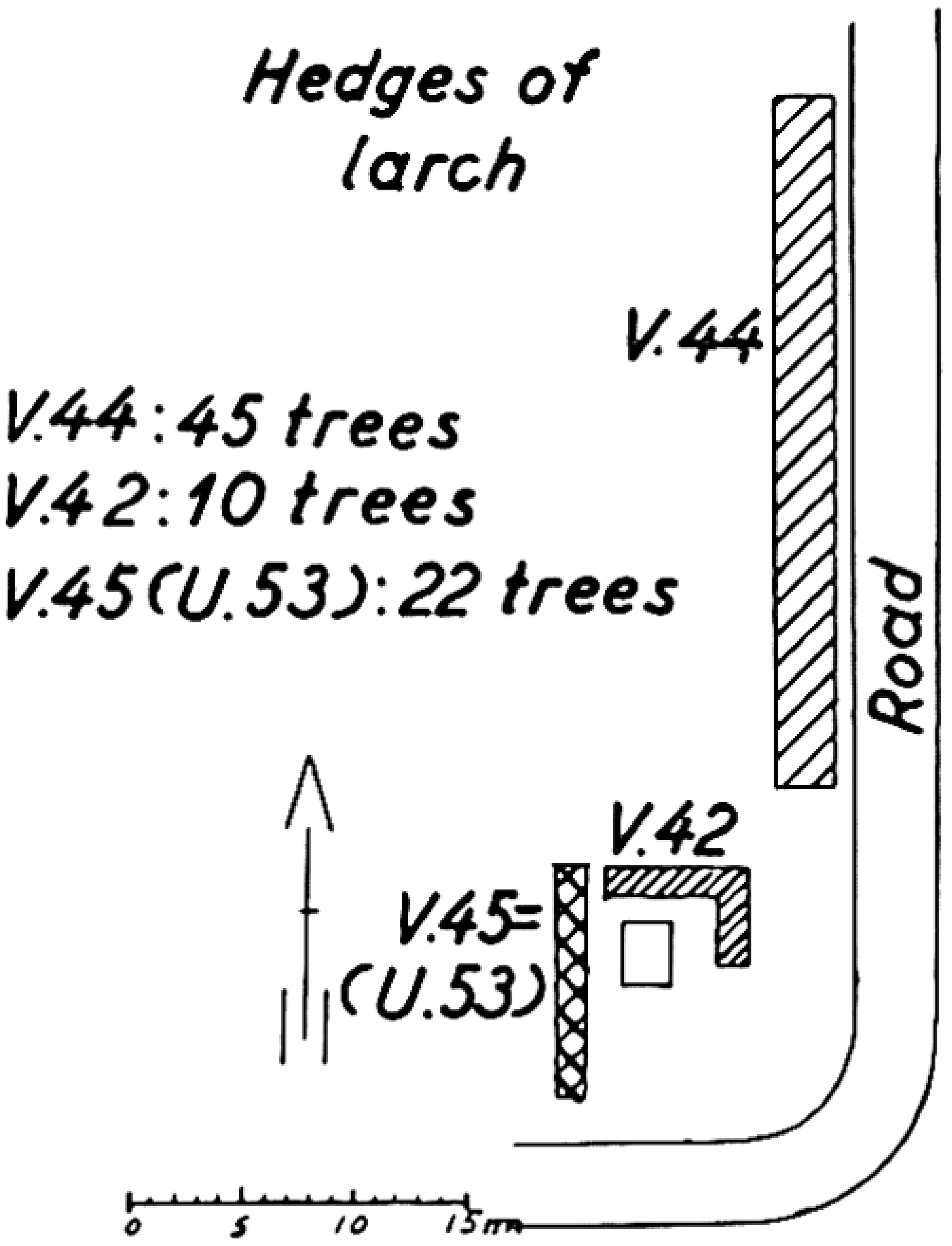


Fig. 39. Location of three hedges of larch, each representing one clone.—V.45: *Larix leptolepis*, 22 grafts from one tree, grafted in 1936.—V.44: *Larix decidua*, 45 grafts from one tree, grafted in 1936–1937.—V.42: The hybrid, V.45 × V.44, 10 grafts from a single plant, grafted in 1936.

The situation with larch is as shown in Fig. 39. Of the three lots, *L. decidua* (V.44) and the hybrid (V.42) have both been heavily attacked by *Chermes*, whereas it is not found on *L. leptolepis* (V.45), see Fig. 40. This shows very clearly that the one selected hybrid plant (V.42), which was chosen as a particularly fine and promising plant, derives its susceptibility to *Chermes* from the *L. decidua* father (V.44). It should further be observed that this *L. decidua* (V.44) was derived from a tree of almost the same age as the old silver fir mentioned above, and has been picked out, moreover, as the finest larch in the country (Fig. 1).

It should further be added that a number of full "brothers and sisters" of V.42, which have had the opportunity to grow on as ordinary trees in another plot, have not shown any significant signs of attack. A hedge consisting of seedlings from the same species cross, and again with V.44 as the father, has, on the other hand, displayed on the whole a great susceptibility to

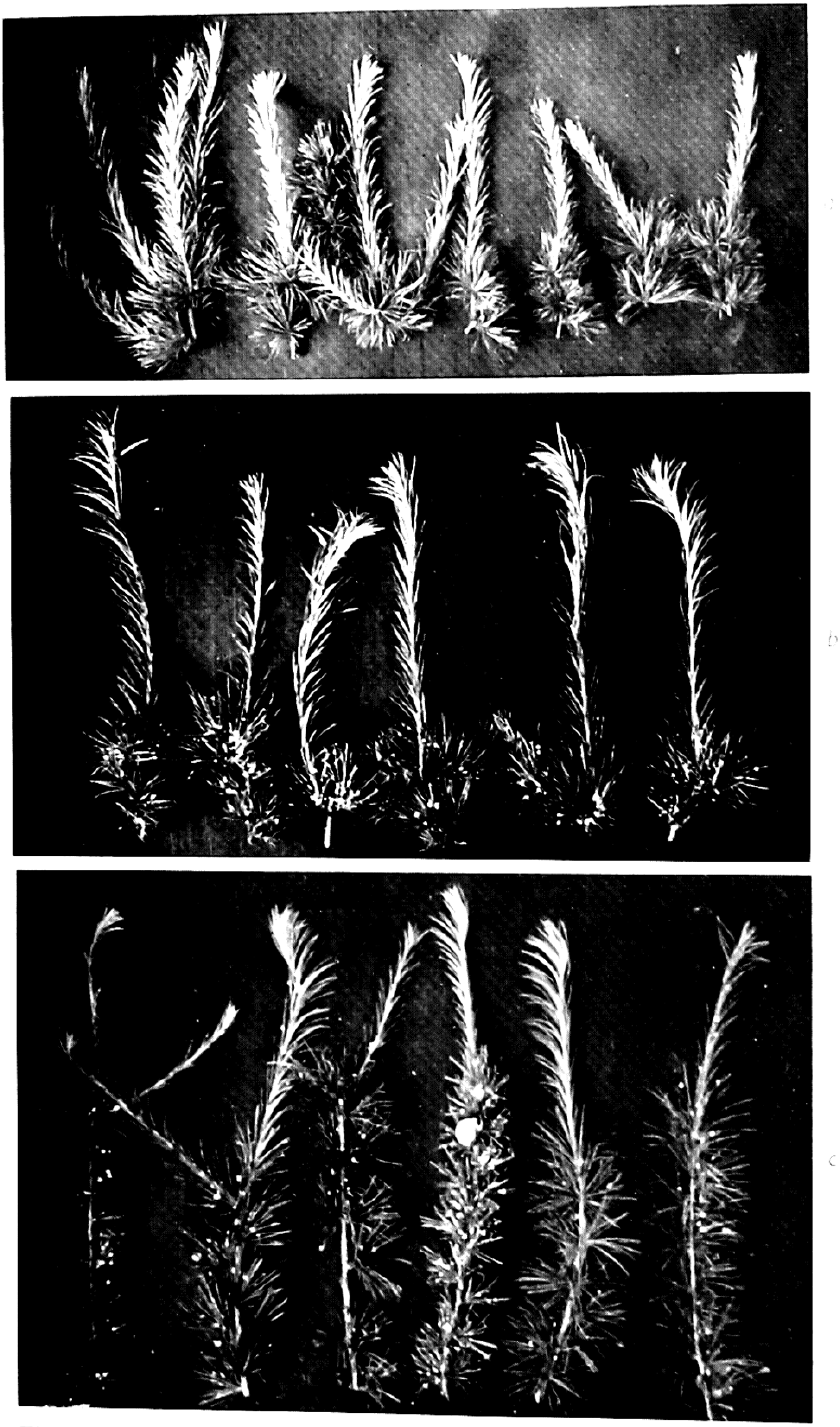


Fig. 40. Shoots of larch. (a): *Larix leptolepis*, V.45 (no *Chermes*) (b) *L. decidua*, V.44 × *L. leptolepis* V.45 = V.42 (*Chermes* present). (c) *L. decidua*, V.44 (*Chermes* present). Photographed on 8th July 1952.

Chermes. This suggests that the mishandling of the plants to make a hedge promotes attack by *Chermes.* It is therefore worth remarking that *L. leptolepis* (V.45), even under these conditions, proves resistant to *Chermes.*

In Scotland and Denmark I have seen *Chermes Cooleyi* occur with special virulence on clipped Douglas firs (hedges). That may suggest that clipping or similar damage can be used more generally as a test of a plant's capacity to resist *Chermes*, and perhaps even other pests.

Another example of attack by insects on clones of larch has been found by us in some graftings of 1943. The clones were placed on several rows of ten-year-old well-grown larch. In each row the trees were headed back to about the height of a man, and on the surface of the wounds grafts were made, each row having its own clone. That is, a tree-show was established in conditions which had previously shown themselves to be suitable for the cultivation of larch.

Included in the experiment, amongst other clones, were three clones of Scottish larch, which had been chosen from a Danish sample-plot. Seven samples of each clone were grafted, and the three clones happened to stand side by side. In the early years they all grew with no external injuries, but in the summer of 1946 one (the intermediate) clone was attacked by a moth, which damaged the leader. This had an extraordinary appearance from the fact that all the leaders in the one row (clone V.629) had snapped, whereas not a single one was damaged in the two adjoining rows of the two other Scottish larches (V.628 and V.630). Although we do not know what it is that has been so attractive in one of the clones, nevertheless there is a warning for the breeder when he sees such an occurrence. It recalls to mind the hares, which relished the bark of different kinds of apples. Professor K. Gram has drawn my attention to the gall *Pemphigus spirothecae*, which is a distinguishing feature of *Populus nigra* and its varieties. In this country this characteristic gall is found only on the black poplars, on which it is common and helps to make identification of the tree-species easy.

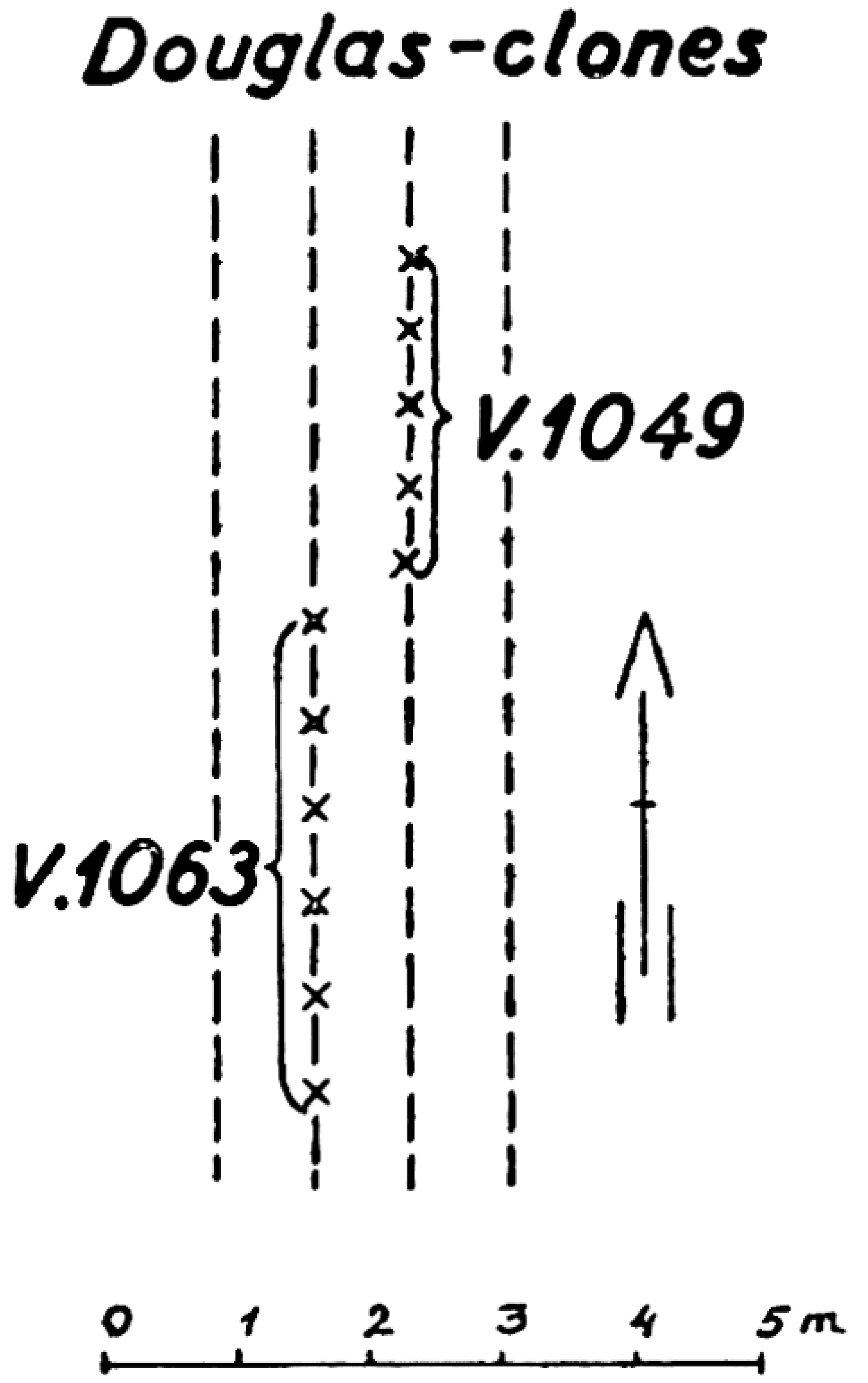


Fig. 41. Location of two clones of Douglas fir.—V.1049: Gold River, Vancouver Island.—V.1063: Wind River, Washington.

For Douglas fir, one example with two clones may be referred to, which was grafted in 1946 and in the autumn of 1952 was standing planted out, as is shown in the sketch in Fig. 41.

V.1049: Grafts from a tree beside Gold River, Vancouver Island. There are five plants with heights: 1·80; 1·80; 1·50; 1·85; and 1·90 m.—mean height 1·77 m. (5·80 ft.).

V.1063: Grafts from a tree beside Wind River, Washington. There were six plants with heights: 2·05; 2·90; 2·80; 2·80; 2·95; and 2·90 m.—mean height 2·73 m. (8·95 ft.).

They thus showed a striking difference in height. If the first plant of V.1063 is not counted in, the difference becomes still greater. This would be quite permissible, as it has certainly made rather an unfortunate start. In addition to the difference in height, it may be mentioned that V.1049 was of excellent uniform growth, whereas the plants of V.1063 were all bent and of bad form as regards the leader, which was also too rampant.

In addition there was something which in this case is most important for us. All five plants of V.1049 were severely attacked by *Chermes Cooleyi*, whereas it was not seen on any of the five plants of V.1063 (see Fig. 42). Both lots were grown in the Arboretum here, after the arrival of the scions in the spring of 1946 directly from trees in stands on the west coast of North America. They had, however, stood so long on the spot where the observation was carried out, and, moreover, they stood there so close beside other Douglas fir clones more or less attacked by *Chermes Cooleyi*, that they should have been equally liable to infection.

When *Chermes Cooleyi* attacks the single individuals in our forest stands of Douglas fir to a varying degree, the above small experiment seems to justify the assumption that it is to some extent due to inherent tendencies. The strongly attacked trees (clones) ought not therefore to be introduced into our seed-gardens.

In further confirmation of this some observations may be quoted from a rather older research area, where there have been grafted clones of Douglas fir since May 1943. A start was made there in a plantation about eight years old, which consisted of a mixture of very varied forms from the greenest and most vigorous to grey and slow-growing individuals. The stand was strongly attacked throughout by *Rhabdocline pseudotsugae* and *Adelopus* (*Phaeocryptopus*) *Gäumanni*, the former confining itself to the blue and grey forms, whereas the latter is a danger to the green Douglas fir, in this country at least.

With the presence on the spot of these two fungi it is possible to test the behaviour of the clones used in grafting towards their attack. No *Chermes Cooleyi* was seen on the area at the beginning of the experiment. It was found in Denmark for the first time in 1938 (MATHIAS THOMSEN: "Douglasgranlusen (*Chermes Cooleyi*)," *Dansk. Skovforenings Tidsskr.*, 1940). It has

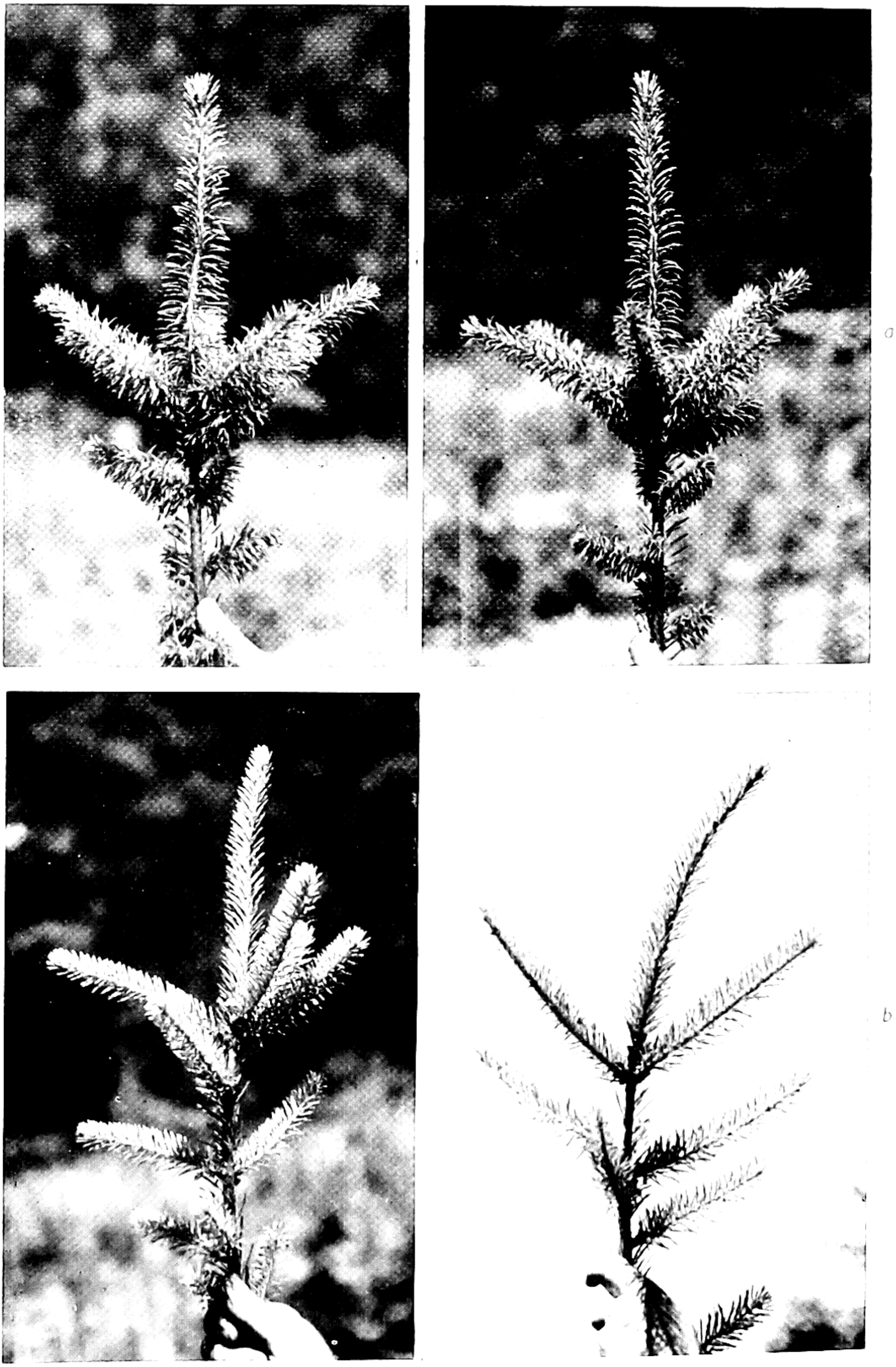


Fig. 42. Top shoots of two clones of Douglas fir. (a) V.1049 (*Chermes* present). (b) V.1063 (no *Chermes*.—All grafted in 1946 and photographed on 9th July 1952.

developed strongly later, however, on this research area as well as on other sites in the country.

Dow V. Baxter, Ann Arbor, Mich., U.S.A., visited the area in the summer of 1950 and took the picture which is used as Fig. 178 in his *Pathology in Forest Practice*, 2nd ed., 1952. It is a similar picture to that given here in Fig. 43.

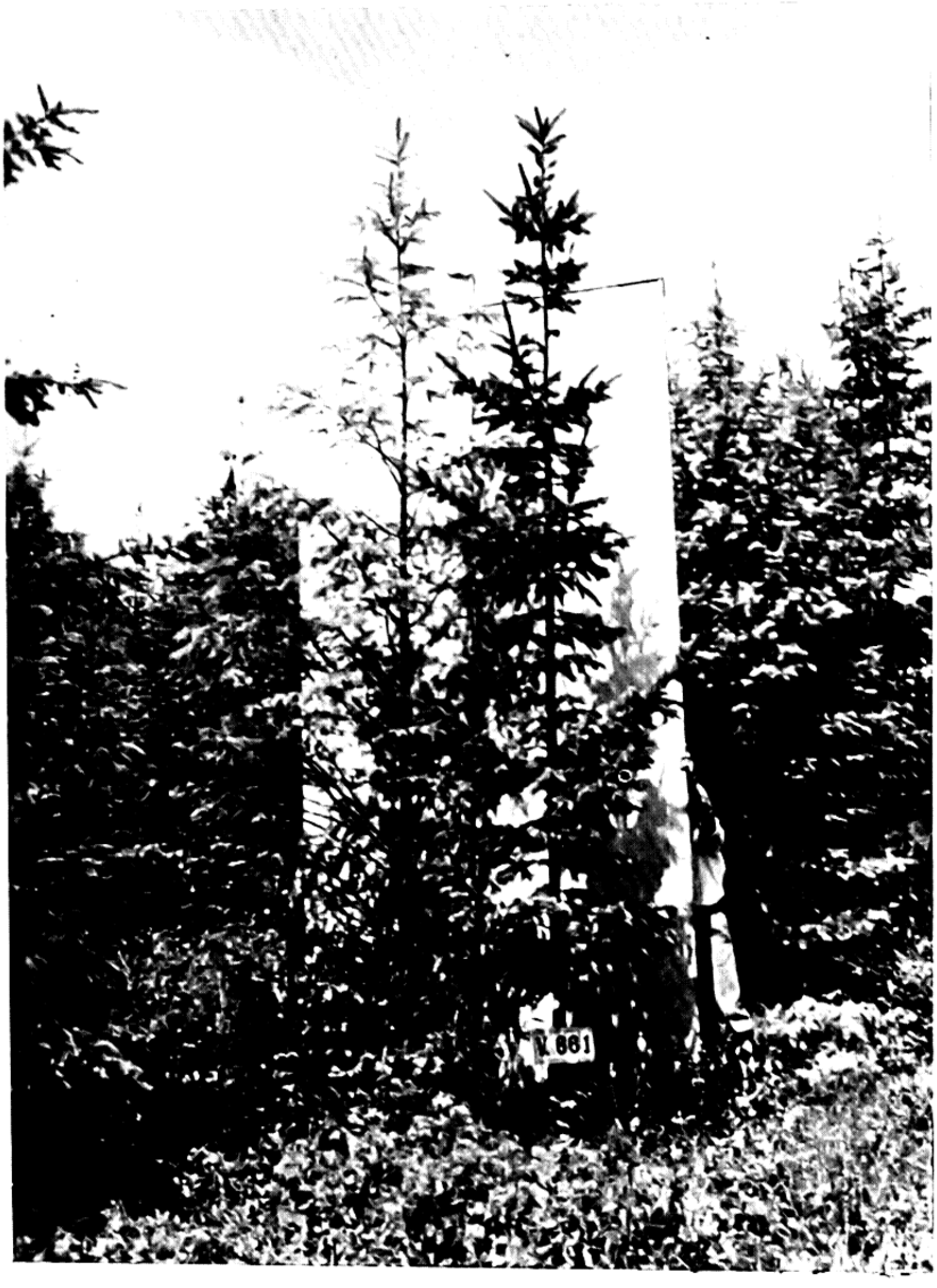


Fig. 43. *Douglas fir*. Testing of one clone, V.661, by grafting in a stand severely attacked by *Adelopus Gäumanni*. *Right:* One tree of V.661, grafted in 1943. *Left:* Original seedling. Photographed on 26th June, 1950.

The picture shows a clone (V.661) from a specimen of Douglas fir found in this country. After having stood as a grafted clone for six years by the side of one of the original ungrafted plants of the stand, severely attacked by

Adelopus (*Phaeocryptopus*) *Gäumanni*, it was still healthy. All the individuals of V.661 have always been unaffected by both *Adelopus* (*Phaeocryptopus*) and by *Rhabdocline* on this site, where throughout a number of years there has been every possible reason for infection.

With regard to *Chermes Cooleyi* the position has been rather different. Clone V.661 is not resistant to its attack. *Chermes* lives on it, but the tree does not seem to be affected by it. In the early years after *Chermes* had begun to show itself in the stand, we saw very little of it on V.661. In the summer of 1952 we had in this country an exceptionally severe *Chermes* year, which also included *Chermes Cooleyi* on Douglas fir. Under these circumstances V.661 also had a heavy stock of *Chermes*, but the clone continued to be vigorous in growth and was clearly distinguishable from the other trees on the area.

The experiment shows that it may be of value to have fungi and vermin within the borders of the country, so that we may have an opportunity to follow, under the local conditions, the reaction of the trees to attack by such pests. Through control of seed and plants, attacks may be checked, at least for some time, and one should not of course deliberately bring in diseases. At the same time, and particularly so in forestry, one should be aware that it may be valuable to make preliminary experiments at an early date in order to be able to arm oneself against the spread of diseases. The forester must not despairingly throw away a new and promising tree-species on the grounds of the initial, perhaps violent, incidence of a disease.

On the Douglas fir research area mentioned there are only grafted clones from trees which were promising for use in forestry. No blue or grey forms were used, and none of the green has been attacked by *Rhabdocline pseudotsugae*.

In connection with the above experiment the question may be asked, whether the root—or to put it more precisely, that part of the original tree lying below the point of grafting—may not have some effect upon the capacity of resistance of the grafts. To throw some light upon this the following experiment may be referred to.

A good 20-m. (65½-ft.) specimen of *Pseudotsuga taxifolia* var. *glauca* stands in the Forest Botanical Garden, which is an older establishment belonging to the Arboretum. The tree was planted in 1889 and is distinguishable from other examples of the type in this country by a vigorous growth unattacked by *Rhabdocline pseudotsugae*, in spite of the fact that the disease for the last fifteen to twenty years has been present in the establishment in question. Only about 50 m. (55 yds.) from this tree stands a Douglas fir of the bluish-grey type from Yellowstone National Park, now twenty-nine years old, and it has been regularly and severely attacked by the fungus. It should therefore be possible to call the old vigorous tree resistant to *Rhabdocline* *pseudotsugae.* A trial, however, with only some few graftings in a tree-show, reveals a rather different position.

On vigorous, typical green specimens of Douglas fir, planted out five or six years earlier, some twigs of the old *Pseudotsuga taxifolia* var. *glauca* from

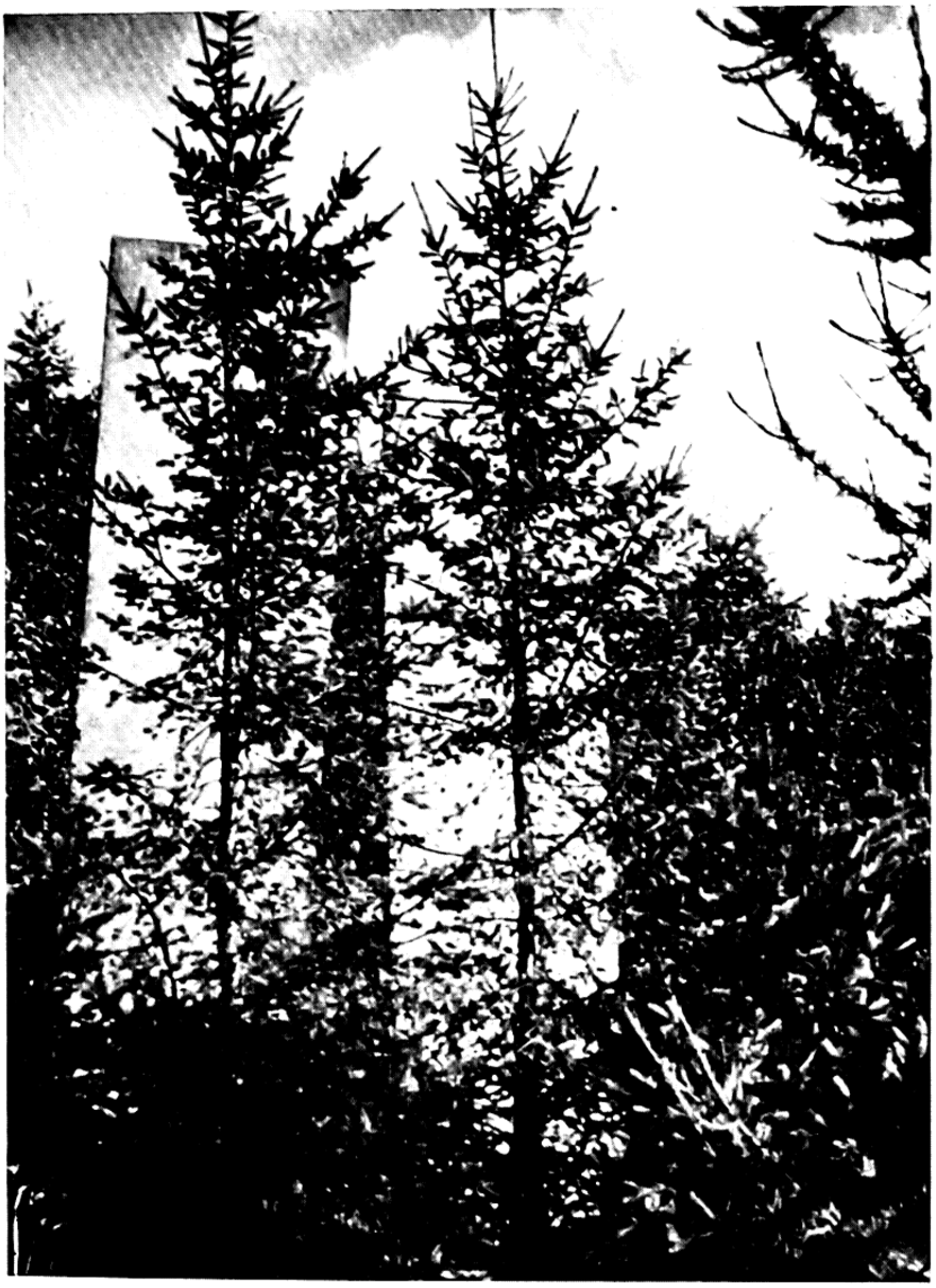


Fig. 44. *Douglas fir*, blue strain. Grafts from one tree made in May 1943 and photographed on 1st September 1952. Severely attacked by *Rhabdocline pseudotsugae.*

the Forest Botanical Garden were grafted in May 1943. In the early years after the grafting the scions grew into strong, distinctly blue and quite healthy new specimens, which appeared as deep blue small trees forming the tops of the green Douglas firs headed back to about 1 m. (3 ft.) above the ground.

After some years of successful growth they were suddenly and severely attacked by *Rhabdocline pseudotsugae*. The attack has subsequently been repeated every year to the same degree on all four grafts, which together make up this small tree-show. Later in the summer they stood almost deprived of all their needles with the exception of those on the last annual shoot, and thus presented a picture typical of the disease. (Fig. 44.)

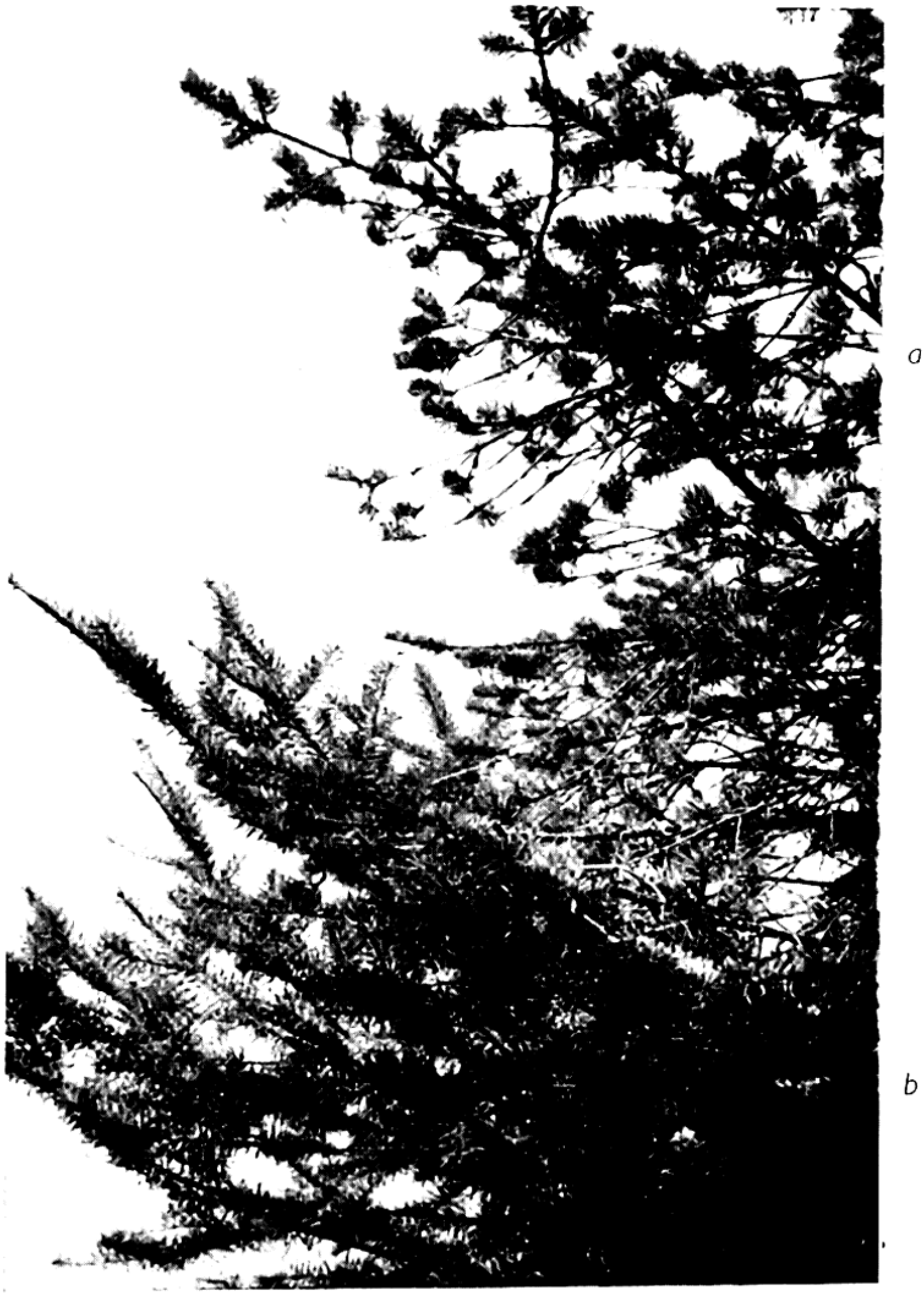


Fig. 45. *Douglas fir*, blue strain (a) (*Rhabdocline* present), grafted in 1943 on five-year-old Douglas fir, green strain (b) (no *Rhabdocline*). Photographed on 26th August 1952.

There is no sign whatever that they recover more easily from the disease through being grafted on vigorous green Douglas firs. In addition to the fact that the grafted blue Douglas fir has obtained freedom to grow more freely and retained all its side-shoots, the branches on the stocks have also been preserved in order to make them as strong as possible, and in order to get the best contrast between the two types of the same species united in one plant.

As is shown in Fig. 45, the blue Douglas fir occurs as the diseased portion above a thriving healthy lower portion of obvious green Douglas fir, which very characteristically has some *Chermes Cooleyi*, but no *Rhabdocline pseudotsugae*. The blue " leader ", which has been ravaged by *Rhabdocline pseudotsugae*, has, on the contrary, not a single *Chermes Cooleyi*. An extremely sharp limit is apparent, which does not furnish any basis for the assumption that " parts " of the trees would affect one another.

This is in harmony with the other observations which have been made in the Arboretum about the grafting of several clones even on rather dissimilar populations. (See also the chapters on " vegetative propagation " and " tree-shows ".)

If we turn back to the old *Pseudotsuga taxifolia* var. *glauca*, now sixty-six years of age, it is striking that the tree has not been attacked by *Rhabdocline pseudotsugae*, when the disease for several years has been on the spot in the immediate vicinity of the tree. This is all the more remarkable because, as has already been mentioned, for more than twenty years the disease has done wholesale damage in Denmark, and graftings of the clone have been seriously attacked after the passage of a few years.

This may indicate that we should be careful in regarding such an old tree as resistant, although it is not attacked in its present form. It may mean that we have been free of the disease in the time of its youth, when the tree was growing in the Forest Botanical Garden. *Rhabdocline pseudotsugae* was found for the first time in 1922 in Scotland, and was not observed in this country prior to 1929. Right up to that time we had in the forest not a few very vigorous plantations of blue Douglas fir, which were all, however, a good deal younger than the tree in the Forest Botanical Garden. From the start which the tree had obtained, it had perhaps escaped the dangerous age, and had thus attained such development of vigour and such an age that it could no longer be damaged. Should that be the case, we should be rather cautious, too, in evaluating old examples of other species, which have arisen under similar conditions.

On *Thuja plicata*, Western red cedar, over a long series of years we have had unpleasant attacks of *Didymascella thujina*. It is at the same time a tree which is easy to work with, because it reproduces itself with no great difficulty from cuttings. It is thus a good research material, as one can operate with complete clones. By using cuttings we have secured the production of some clones, which clearly show evidence of resistance by the plants and the utility of the method in assessing their forestry value.

One clone, V.469, which was planted on two small research areas in the Arboretum, is particularly promising. On both sites it was planted with cuttings made in the spring of 1942. On one of the areas it is compared with cuttings of the same age of a second clone, V.470, whereas on the other area it is planted beside seedlings of the same age.

An assessment of the ten-year-old experiment gave the following figures:

Area I
Clone V.469: mean height 6·8 m. (22·2 ft.)
Seedlings: ,, ,, 5·1 m. (16·9 ft.)
Area II
Clone V.469: mean height 6·3 m. (20·7 ft.)
,, V.470: ,, ,, 5·2 m. (17·1 ft.)

All the plants started off at the same time and must be considered to have had the same opportunities for their development, so that the different height-growth is very striking.

It may be added that clone V.470, which has not grown so well, originated from an otherwise promising tree in the same family of brothers and sisters (plants with a common mother), from which the seedlings used were derived. That family consists of a group of fine trees, which stands in good conditions in the Forest Botanical Garden, and originated from seed harvested in 1906 from an old tree in the same institution. They should therefore be as well adapted to our conditions as it is possible to imagine.

If we leave the seedlings out of the comparison, as they represent a different method of propagation, and confine ourselves to the cuttings in the two clones, we again notice a considerable difference. Clone V.469 has all the time been untouched by frost and *Didymascella thujina*, whereas there is distinct evidence of both in the poorer clone, V.470, which has, however, been damaged by frost in the first instance.

The valuable clone V.469 was taken from a tree which, on its growth-site in the forest (Linå Vesterskov in Midtjylland), did not show any marked evidence of vigour. It is not a very large tree for its age, but it is standing on a rather unfavourable growth-site for the species. Directly after some exceptionally severe winters in 1939–1942, it stood, however, as the one specimen on the site with fresh green colouring right to the top, and led one to suppose that it was the possessor of exceptional hardiness. It is perhaps that feature which primarily determines the outstanding growth of the clone. In this country it may be that the usually rather severe attacks on young thuja by fungi are primarily due to the low suitability of its plants for our climate. Accordingly, attack by *Didymascella* might be said to be essentially secondary.

What has been mentioned above cannot in any way claim to be an experiment which can clear up the various problems concerned with the injuries in question. The concept of " diseases " is here a very broad one, so as to comprise attacks by fungi, insects, and frost. In practical forestry as well as in forest-tree breeding it is often difficult to keep these problems apart; but they are of equally great importance. It is certainly important to know what is inheritance, and what is "false inheritance"; for the sake of practice one must pay equal attention to both things. A forest genetical elucidation may be protracted; but that does not always mean that the breeder needs to await the result before he attacks it from his side.

For plant pathologists and forest zoologists the demand must be for much more far-reaching research. In between laboratory investigations and the tree-shows mentioned it will often be advantageous to insert experiments which can be carried out at research stations.

As an example reference may be made to a fungus like *Chrysomyxa abietis* on *Picea Abies*, where it has not been made clear whether the attack is determined by the different flushing time of the individuals, or whether they get their individually determined capacity for resistance in some other way. As a link in such an investigation it may be a question of producing sets of clones growing in flower-pots, so that each set has its own time of leaf-flushing. This can be brought about by moving them in lots into the greenhouse at different times. I have attempted this on one occasion, when the result was checked by N. FABRITIUS BUCHWALD. Four sets with twenty-five plants in each set were used from two clones. It was encouraging to the extent that neither of the two clones was infected, after all the plants had been placed beside a diseased stand. As an experiment it had the defect that a clone was not at the same time included, the susceptibility of which was known.

Reference should also be made to the experiments by W. v. WETTSTEIN. He collected seeds of a few *Picea Abies* (Norway spruce) which had been spared during an attack by the nun-moth which ravaged about 2000 ha. (5000 ac.) of spruce forest in eastern Prussia in 1934–1935. In the progeny of these selected trees were found plants which the larvae of the nun-moth would not feed upon. (W. v. WETTSTEIN: "Skogsgenetiska undersökningar," *Svenska Skogsvårdsföreningens Tidskrift*, 6. 1947.) These experiments were very encouraging. They have now been ruined by the last war; but when they or similar experiments are again taken up, it must be recommended that they should be combined with use of vegetative propagation.

The most frequently quoted example of the ravages of a forest disease is of course *Cronartium ribicola*, which invaded the forests of White pine (*Pinus strobus* and *P. monticola*) in North America. From the forestry aspect it was this example which in the first instance contributed to the setting-up of control of plant diseases. The fungus is thought to have been carried into North America on plants of *Pinus strobus* from European nurseries, where they had been infected from *Pinus Cembra*.

Cronartium ribicola lives on *Pinus Cembra* without causing trouble; but when it slipped into North America it encountered in *Pinus strobus* a tree-species liable to its attack, which had at the same time already been taken into cultivation in Europe. The result was violent attacks both in North America and in Europe.

In the east of North America the attack began on *Pinus strobus* and then travelled disastrously across the U.S.A. and Canada, and is now advancing in the virgin forests of *Pinus monticola* of the Pacific Coast. The progress of the disease has been so swift that it has become the general opinion that the only hope of restricting the calamity is by eradicating all *Ribes*, which is an essential intermediate host of the fungus. Unfortunately, besides being cultivated, *Ribes* is also very widespread in the North American forests, where very large sums were spent in combating it in the hope of thereby saving the White pine.

There has formerly been discussion as to whether there might be any hope of finding within *Pinus strobus* resistant individuals or types, so as to lead to the disease being fought in that way. (Cf. H. VAN VLOTEN: *Nederl. Boschb. Tijdschr.*, 1939, pp. 501–512, and 1941, pp. 345–346; J. S. BOYCE: *ibid.*, 1941, pp. 173–182.)

The work of breeding for resistance was taken up with great energy by A. J. RIKER in Wisconsin, on the basis of trees within the natural range of the species. In the course of about ten years 163 trees had been brought into the work, which consisted of about one thousand grafts and about ten thousand seedlings collected in " the blister rust nursery ", as a section of the Griffith State Nursery.

In 1948 RIKER reported: " The grafts have stood up against extremely severe inoculation in a way that is really encouraging. The evidence available all indicates that we have some resistant White Pines " (A. J. RIKER: " Developing Resistance to Disease in Trees," *Proceedings of the 24th National Shade Tree Conference*, 1948). Reference may also be made to similar results got by HIRT in New York (RAY R. HIRT, 1948: " Evidence of Resistance to Blister Rust by Eastern White Pine growing in the North-east," *Journ. of Forestry*, Vol. 46, pp. 911–913), by HEIMBURGER in Canada, and to a general reference to the problem in RUSSELL B. CLAPPER, and JOHN M. MILLER: " Breeding and Selecting Pest-Resistant Trees," *Yearbook of Agriculture: Trees*, 1949, Wash., D.C.; and ARTHUR HARMOUNT GRAVES: " Forest-Tree-Breeding," *Economic Botany*, 1948.

In a later report mention is made of satisfactory results from raising *Pinus strobus* by cuttings in order to progress in that way to making use of the results. (J. E. THOMAS and A. J. RIKER: " Progress in Rooting Cuttings of White Pine," *Journ. of Forestry*, 1950, Vol. 48, pp. 474–480.)

It is not surprising that such excellent results have further stimulated the work. It has later, from about 1947, been taken up as a large-scale task in North-western Project: " Blister Rust Control, Spokane, Washington," where it is primarily concerned with Western White pine (*Pinus monticola*).

In an article by R. T. BINGHAM, A. E. SQUILLACE, and J. W. DUFFIELD (" Breeding Blister-Rust-Resistant Western White Pine," *Journal of Forestry*, 1953, Vol. 51, pp. 163–168) there is a report that they have found there in the course of a few years a number of individuals which furnish convincing evidence that they are resistant. Moreover, mention is made in it of an elaborate programme for further breeding work, which, as in RIKER's case, comprises both seedlings resulting from free pollination and grafts from selected trees, as well as the making of controlled pollinations. All are subjected to artificial infection. Stress is also laid upon the opportunities, afforded by the breeding, of being at the same time able to arrive at a use of those trees which, owing to their constitution, are best from a forestry viewpoint.

In addition to these very encouraging results it is, however, not out of place to refer here to the fact that the work can also be taken up in regions where *Pinus strobus* does not occur naturally. This can be done in several places in Europe, where it was introduced early on, and for a shorter or longer time raised hopes that something valuable had been brought in.

About two hundred years ago *Pinus strobus* was introduced into European forestry and was soon regarded with much interest. It did not take long, however, before *Cronartium ribicola* set in with such virulence that on the whole its planting had to be given up. Scattered over European countries there are to this day large and splendid trees of *Pinus strobus*. These must attract interest for further local use, and by working with them it may be possible to contribute to a better understanding of the problem and to track down material of more general value.

If we have advanced only so far that we can entertain hopes of being able to solve the problem, we must not spare our resources. Seed-gardens, which may give us good White pine, can stand a heavy investment of both labour and money.

The work is heavy, so that it ought to be tackled from several directions—and moreover ecological conditions seem to indicate that the work should be locally distributed. A type which is possibly of use in one locality need not be useful in all conditions. As an example of this it may be mentioned that " Scottish larch " from a particularly fine stand in Scotland also furnished excellent larch in Denmark, where it was, however, completely destroyed by larch canker. Reference should also be made to the fact that in New Zealand there is a considerable stand of *Pinus strobus* about 30 years of age. It is such a fine stand and so remarkably healthy that nothing like it is known in Europe, and it would perhaps be difficult enough to find one in North

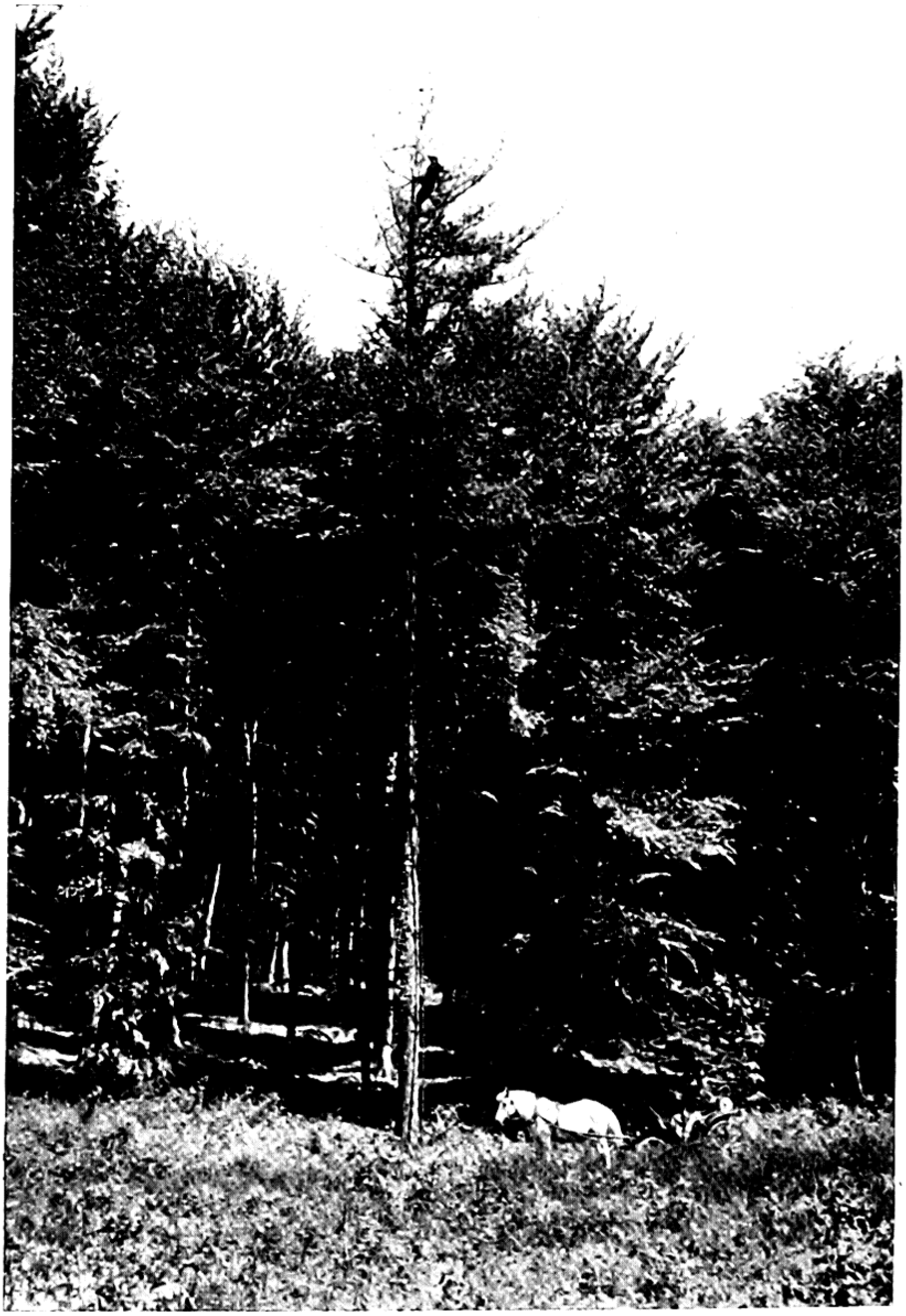


Fig. 46a. Weymouth pine, *Pinus strobus* L. Original tree with bags for controlled pollination, photographed on 31st May 1945.

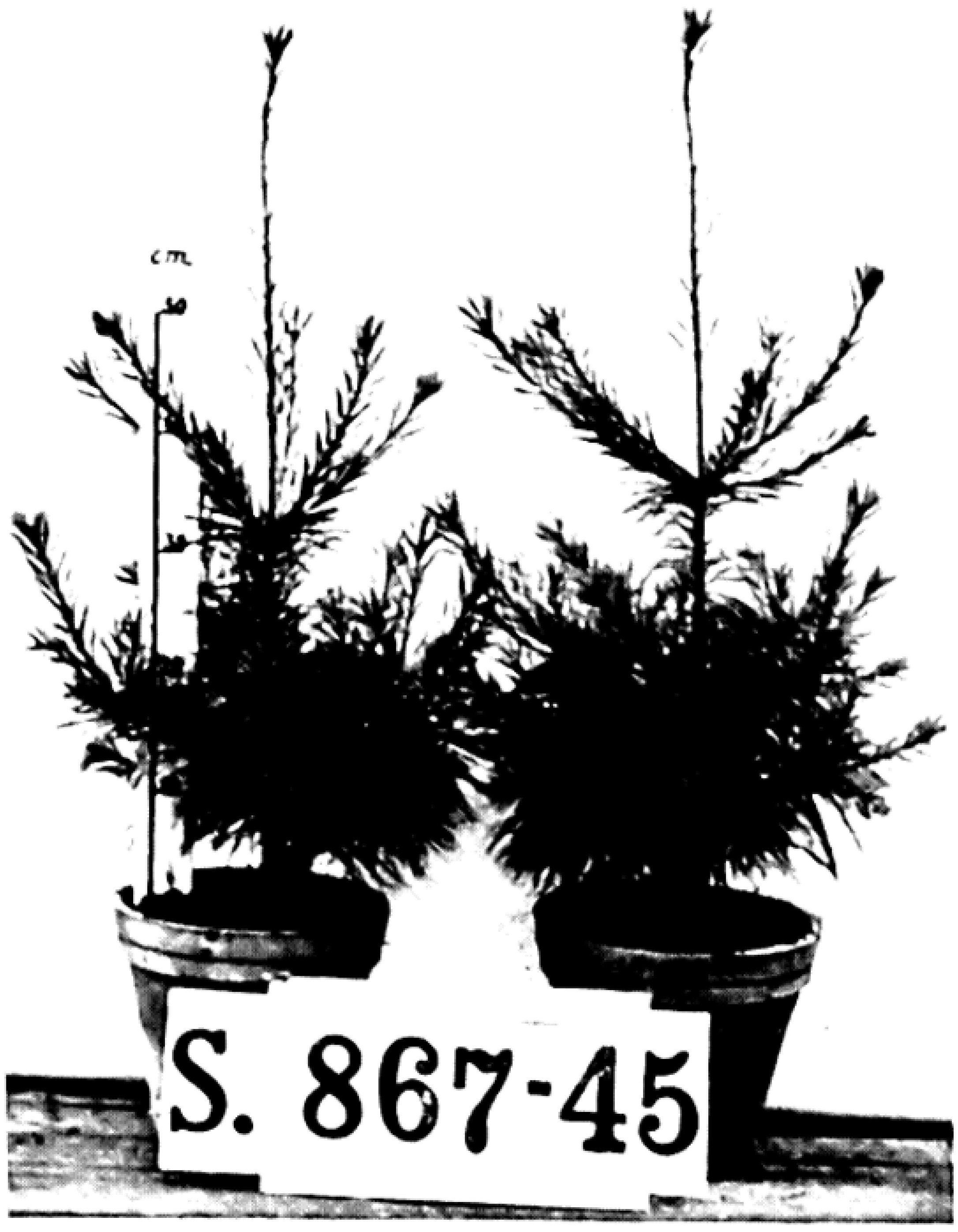
Fig. 46b, c and d. Weymouth pine:

(b) Two seedlings resulting from the pollination in Fig. 46a, photographed on 30th June 1950.

(c) Two grafts from the tree, Fig. 46a, grafted in the spring 1948. Photographed with female flowers (♀) on 30th June 1950.

(d) Three grafts of the same lot, photographed on 8th July 1951. Observe the cones.

b



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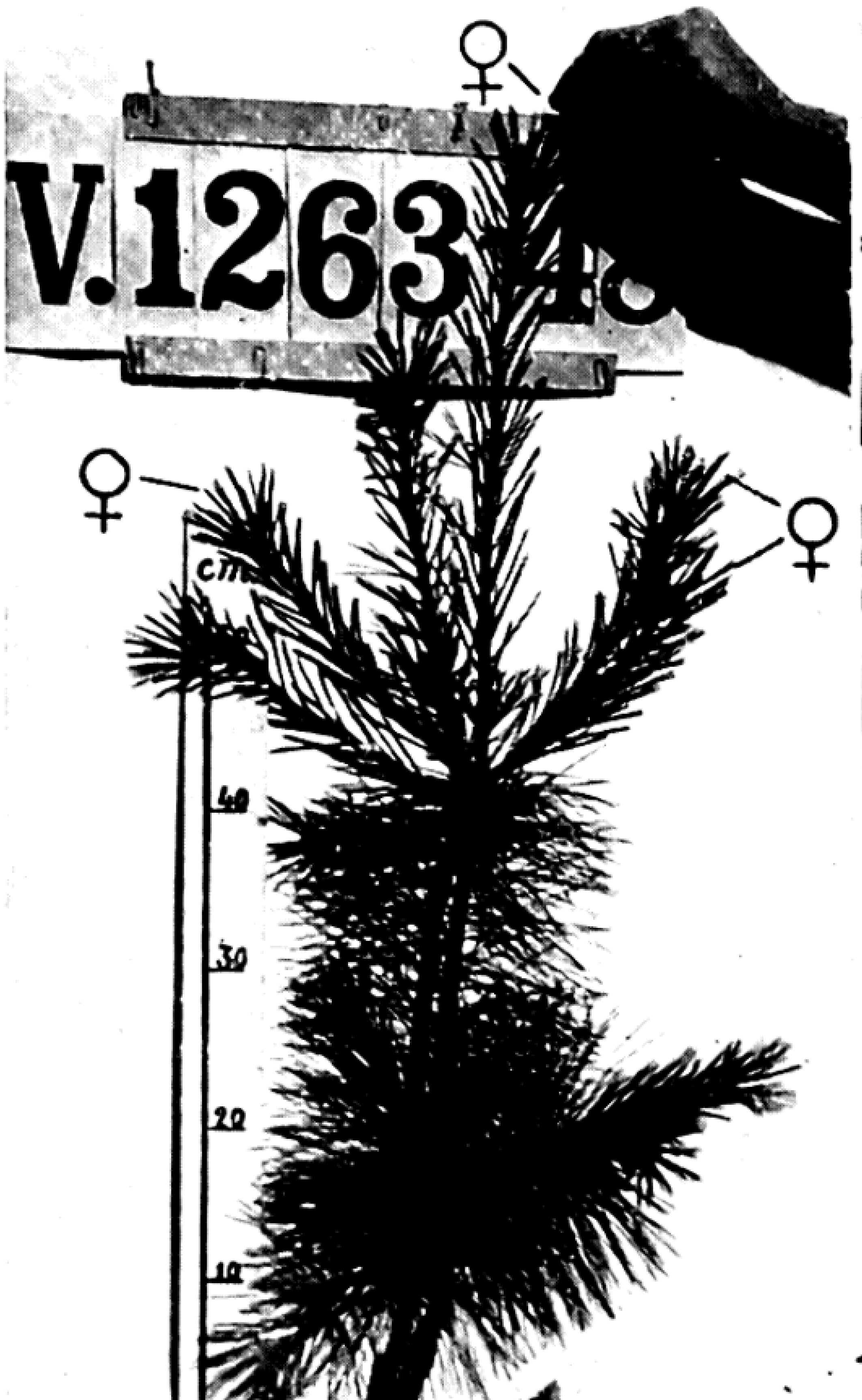
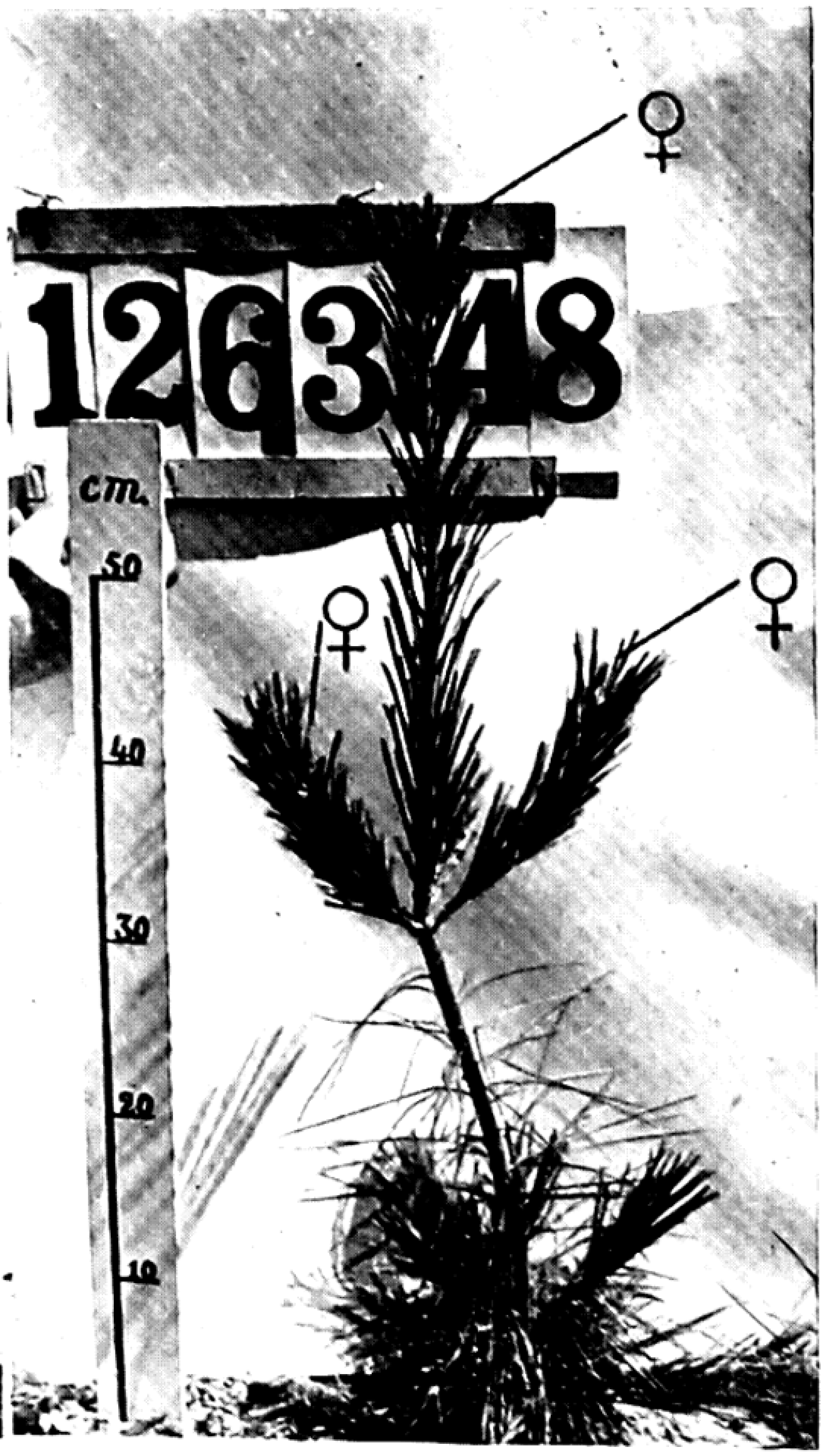




c

America. It should be observed that we do not know whether we should explain this as due to ecological conditions or as the result of isolation. Up till now there is no evidence available for one view or the other.

Apart from the considerations mentioned above, we in this country go in for working with the apparently healthy trees surviving through almost the past one hundred and fifty years, in the hope of raising in that way something valuable for further distribution. By sowing seed from individual trees which have been freely pollinated we have obtained variation in growth for the different progenies. They stand exposed to infection, but whether they have different susceptibility cannot yet be determined. Further, tree-shows have been started with graftings from selected trees, which from historical information appear to have survived severe attack in their immediate neighbourhood. Simultaneous with the establishment of tree-shows some grafts have been picked out for research in early seed-setting.

In the tree-shows the plants should remain as far as possible untouched, so as to attain the most natural growth, which may provide a basis for an assessment of the combination of tendencies present in the individual. Besides using the result of such an assessment of the selected individuals, it would be a great advantage to have at the same time the clones preserved in grafts, which, by repeated transplanting, for example, can be compelled to flower and set seed abnormally early. That will render possible an early and extensive use of controlled pollination, which may provide additional information of the genetical constitution of the trees.

From one clone (V.1263) of *Pinus strobus*, which was grafted in the spring of 1948, it was already possible in the spring of 1953 to sow seed derived from controlled pollination. Some of the clonal plants have borne female flowers four years in succession. The tallest plants are only 3 m. (10 ft.) high, so that it is still very easy to control the pollination. It has even been possible to get flowering in the same year in which the grafting was done in the early spring, and in the following year to have ripe cones with seed. This agrees with results from graftings of other species of *Pinus*, but is mentioned merely because it may be some encouragement in the work. There is, of course, not much practical significance in intensifying breeding for seed to that extent. If we are allowed to take only four or five years in order to make the controlled pollination on material propagated vegetatively, even that would be a considerable advance. It will certainly be appreciated by those who have personally had to make pollinations in tall old trees, to reach which they may, in addition, have had to make a long and wearisome journey.

By combining the employment of tree-shows and the use of grafted plants along with early seed-setting with controlled pollination, we have a valuable technique for later work. This may not only demonstrate a possible resistance to *Cronartium ribicola*. It will also be work which leads on directly to a use of the results for application in forestry.

As the result is not certain, and it will always be wise to keep several possibilities open, reference must also be made to the opportunities for resistance breeding by using hybridization with other species. For this *Pinus peuce* has been used.

In the example of hybrids between *Populus tremula* and *P. tremuloides* mentioned earlier, we get (as in the better-known case of crossing between *Larix leptolepis* and *L. decidua*), besides the increase in growth-energy, resistance to serious fungous disease. The problem will therefore be dealt with in more detail in the next chapter. In this chapter the aim has merely been to stress the importance of the use of vegetative reproduction as a technical aid. (C. SYRACH LARSEN: " Studies of Diseases in Clones of Forest Trees," *Hereditas*, 1953, pp. 179–192.)

It may sound paradoxical that it is better to keep one's enemies alive than to exterminate them. In considering this matter it must be mentioned, however, that by eradicating a harmful insect we also wipe out its natural enemies. From nurseries, we know that great advantage is derived from sterilization of the soil to kill all fungi. It also involves a great risk that a single fungus may gain access and attain to an explosive development, as " the land lies open " because of the exclusion of the competitors by the previous heavy-handed treatment of the soil.

We must not make our forests too uniform, and we must avoid any unnecessarily severe interference with nature's housekeeping; but from that to " leaving things alone " is a big jump. For purposeful and sound breeding in the future campaign against attack by disease, there is still a wide field of work ahead of us.

When now and then we deem it advisable to powder whole areas of land with poison in order to combat a particular pest, the feeling may not be wanting that it is a desperate treatment, which has become popular at a time when little has been done to attain a deeper understanding of the complex character of the problem. It is high time that we foresters tried to attack the problem from another aspect so as to avoid at least an unnecessary cultivation of the weak.

CHAPTER IX

HYBRIDS

THE first instance of hybridization which really attracted forestry interest was the cross between the Japanese and the European larches. The hybrid was of vigorous growth, but it was mainly its capacity for resistance to the dangerous "larch canker" which created a stir. *Larix eurolepis* Henry got its name from *L. leptolepis* and *L. Europaea* (= *L. decidua*). It was described for the first time from Scotland, where in preceding generations there had been rather heavy losses caused by ravaging attacks of larch canker (*Dasyscypha Willkommii* (Hart.) Rehm.) on European larch.

In Scotland and in other parts of west and north Europe the European larch (*L. decidua*, Mill., *L. Europaea*, DC.) is a valuable tree with rapid growth, good form, and valuable timber. It is only its susceptibility to larch canker that has contributed to restricting its wider use in forestry. The attacks were so troublesome that in the silviculture of west and north Europe there was a change-over on a large scale to the use of Japanese larch, which in its first trials had proved to be resistant to the fungus. That was the solution adopted, although the Japanese larch had been known in Europe only as a more coarsely branched tree, and in spite of the fact that in Japan it does not grow to such a height as we know the European larch does in Europe. Preference was given to certainty of production rather than to more valuable but less certain production.

It was therefore natural that the hybrid between the two species was followed with great interest, as the first plantations formed on the basis of hybrid seed (which had been produced spontaneously at Dunkeld in Scotland) had already led to the belief that the cross might combine the resistance of the Japanese larch to the fungus with the better form of the European larch—both these things being further emphasized by a considerable hybrid-vigour (heterosis).

On the slopes running down to the park at Dunkeld stood some magnicent hundred-year-old European larches, when in 1905 seed was gathered from a small row of Japanese larches, which had been planted in the park in 1887. The Japanese larches were to a great extent fertilized by pollen from the European larches, and the progeny were used for plantations on the estate and were distributed more widely. The first planting was carried out in 1908 with three-year-old plants. On the whole the individual "age-classes" were kept to themselves in the plantations, in which the surroundings were often filled in with European larch. This gave a strong impression of the forestry value of the hybrids, since the plantations of that tree stood in vigorous growth, whereas the surrounding European larch was severely damaged or almost wiped out after attack by larch canker. " It is exceptionally healthy, comparatively free from *Chermes* attacks, and absolutely free from canker " (J. M. MURRAY, 1915).

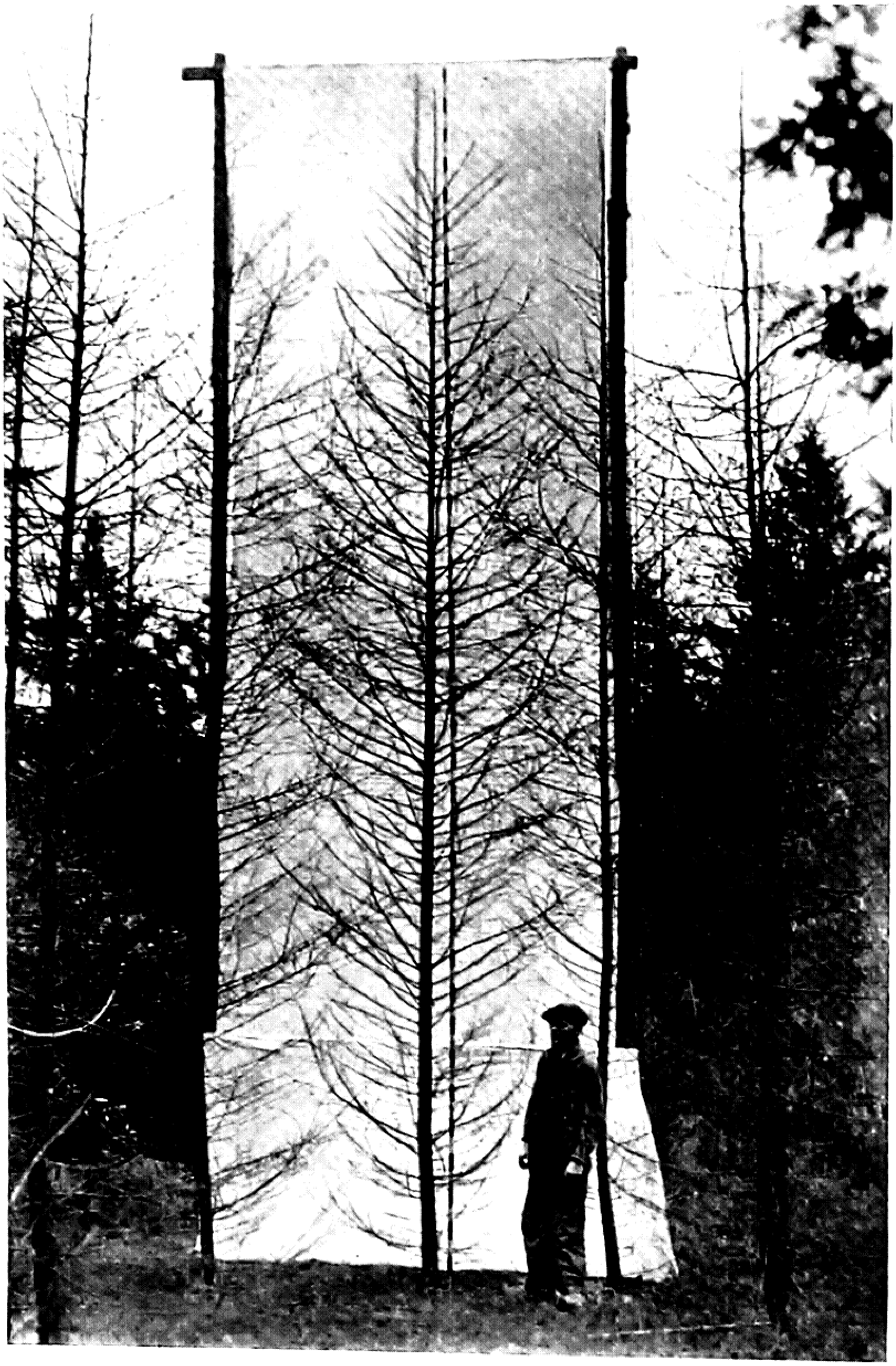


Fig. 47. *Hybrid larch*. Seeds came from Dunkeld. Forest Botanic Garden, Denmark. The finest tree in the stand at 10 years of age. Height—7·5 m. (24·6 ft.). Photographed on 29th April 1936. *See* Fig. 60.

Further information about the larches at Dunkeld occurs in J. M. MURRAY: *Transactions of the Royal Scottish Arboricultural Society* (1915); A. HENRY and MISS FLOOD in *Proc. Roy. Irish Academy*, XXXV, Sec. B, No. 4, p. 58 (1919); E. V. LAING in the *Royal Scottish Forestry Journal*, 1944, and J. D. MATTHEWS in *Forestry Commission Forest Record*, No. 25 (1954).

In this country a small group of progeny from Dunkeld was examined in detail in 1936 when ten years of age. There were in all 113 trees, fifty-six of which were taken out in a thinning at that time. At the assessment the trees were readily differentiated into red-barked and light-barked trees, the former being booked as Japanese larch and the latter as hybrids. This was also confirmed by examination of the colour of the female flowers. It is presumably justifiable to regard the light-barked trees as being the hybrid *Larix leptolepis × decidua*. On the other hand, it is unlikely that there should not be exceptions as a result of unusually odd combinations, and possibly also individuals characterized phenotypically, but this can have no effect on the general result of what, in its whole procedure, was rather a crude experiment.

It is possible that in Japanese larch there are two types, which differ in the colour of their bark, and such that the light-barked one has the better form, possibly a lowland form, as opposed to a redder-barked highland form, in conformity with the variation of colour in the female flowers for corresponding growth-sites, which is known in Japan. Some such thing could explain a case like the foregoing without any assumption of crossing. From the material available in Europe, however, the Japanese larch always seems to have red or reddish-brown annual shoots, which, although the colour of their bark rather varies, are nevertheless clearly distinguishable from the light-coloured shoots of the European larch and of the hybrids produced by controlled crossing between the two species.

With regard to the branch structure a difference was also observed, such that the trees with light bark were from the forestry viewpoint more valuable. Reference need only be made, however, to Fig. 47. This shows the finest tree of the group, which is light barked and in build very reminiscent of a well-shaped European larch. (See Fig. 60, with clone V.414, in the chapter on " breeding of larch ".)

After sorting out the light-barked and the red-barked trees a height measurement gave the following result:

The fifty-six felled trees gave:

	Mean Height	*Greatest Height*
28 light-barked	5·86 m. (19·2 ft.),	8·00 m. (26·2 ft.).
28 red-barked	4·56 m. (15·0 ft.),	6·80 m. (22·3 ft.).

The fifty-seven remaining trees gave:

	Mean Height	Greatest Height
43 light-barked	6·90 m. (22·6 ft.),	8·70 m. (28·5 ft.).
14 red-barked	5·79 m. (19·0 ft.),	7·10 m. (23·3 ft.).

A well-marked height difference is thus evident in the two colour classes in favour of the light-barked ones, which both amongst the thinned-out trees and in the remaining stand considerably exceeded the red-barked in height. Likewise it should be noted that, whereas the ratio between light-barked and red-barked in the thinnings removed (the smallest and in other respects the poorest) was 1 : 1, the same ratio amongst the remaining (better) trees is 3 : 1. This means that already, after a first thinning like this, the light-barked trees are clearly dominant.

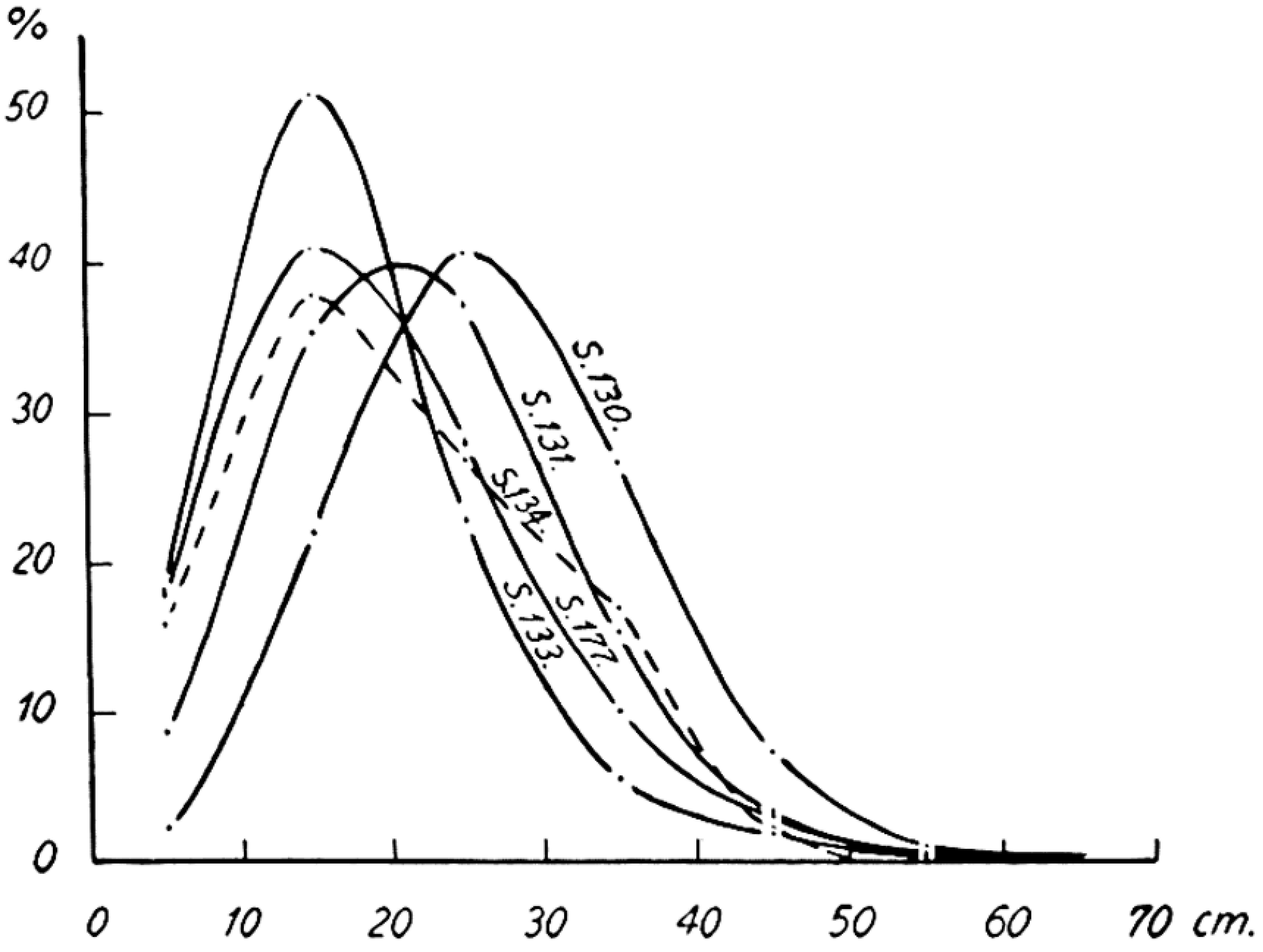


Fig. 48. Height-curves for larch two-year-old seedlings.

At the felling in the autumn of 1940 there remained in the stand:

	Mean Height	Greatest Height
13 light-barked . . .	11·37 m. (37·3 ft.),	13·25 m. (43·5 ft.).
2 red-barked . . .	9·65 m. (31·7 ft.),	10·10 m. (33·1 ft.).

Where the two species are planted close beside one another, the hybrid between them seems to arise very easily. The time of flowering has a considerable effect, however, for it occurs at nearly the same time for both species, but at the same time varies quite appreciably from tree to tree within the individual species. Finally, the relative time for the advent of flowering is also subject to climatic influences. At Dunkeld, progeny which was clearly differentiated was obtained from year to year; use was made of this to sort out the plants in the nursery according to the colour of the bark, so that only the light-coloured were used as hybrids. Notice was taken of this year-by-year fluctuating result at an early stage.

Even as early as in the two-year-old seed-bed plants, an assessment shows what has been the production of hybrids in the particular year, and that the results vary from year to year.

In this connection reference may be made to an experiment in which seed was taken from four trees of Japanese larch, which besides being exposed to pollination from the same species also stood open to receive pollen from a group of European larch. The experiment was assessed in the autumn of 1935 on two-year-old seedlings, for which the height measurements could at the same time be compared with those of Japanese larch of the same age from seed brought from Japan. The result is illustrated in the form of curves, which may be seen in Fig. 48.

In two of the sowings (S.133 and 134) the light plants were only slightly conspicuous, and these beds were in their general appearance not very different from those of pure Japanese larch (S.177), but in the other two sowings there was a very decided difference. These two (S.130 and 131) were very fine beds, with tall, slender, light-coloured plants forming the main constituents. For use in forestry one would undoubtedly prefer S.130 and 131.

By controlled pollination, material is obtained which shows the difference between species and hybrids more clearly and provides evidence of the hybrid-vigour (heterosis) achieved in the process. Fig. 49 shows the different development of plants sown in 1933 and measured at the age of two and three years. On the basis of pollinations, likewise made under control in 1942 (sown in 1943), the following may be quoted:

S.640–/43 = European × European larch;
S.631–/43 = Japanese × European larch;
S.627–/43 = Japanese × Japanese larch.

No.	Measured Jan. 1945	Measured Nov. 1947	Measured Feb. 1951	Measured Jan. 1955
	Ht. in cm.	Ht. in cm.	Ht. in cm.	Ht. in cm.
S.640	43	124	338	643
S.631	80	233	525	909
S.627	66	159	387	690

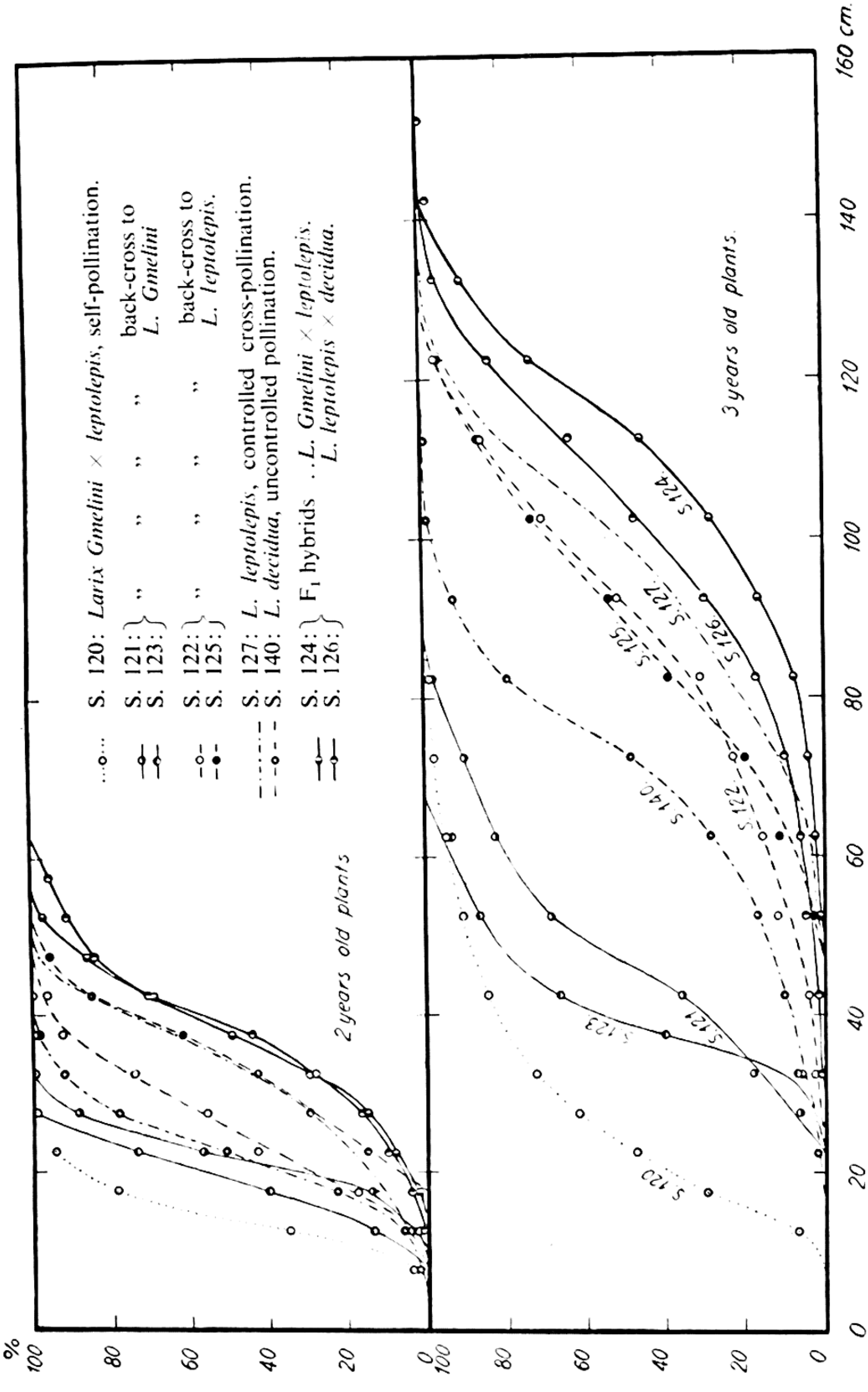


Fig. 49. Height-curves for larch. Controlled and uncontrolled pollinations.

If we combine this evidence that something of value can be fixed in first-generation hybrids with what was said in the previous chapter about vegetative reproduction and seed-gardens, we are at once introduced to one of the most important procedures in planned improvement. There is no need to be satisfied merely with combining the desirable tendencies, as we find them in the individual species. We also have a great opportunity to combine tendencies from different species in one and the same progeny for direct use in forestry practice. By taking advantage of long-lived individuals in the formation of our seed-gardens we have in forestry the unique opportunity to utilize just that kind of improvement—a combination of hereditary tendencies (genes) from different species with hybrid-vigour (heterosis).

The event reported by H. H. CHAPMAN concerning *Pinus palustris*, Mill. × *taeda* L. (H. H. CHAPMAN: " A New Hybrid Pine," *Journal of Forestry*, 1922), which from the first report seemed to be promising, but at a subsequent trial proved to be less valuable by, amongst other things, having inherited the sensitivity of one of the species to forest fire, must on no account induce us to give up the use of hybrids. It merely illustrates clearly one example of inheritance from both sides. In this case it happens to be a poor quality; but it is on that account just as valuable for illustrating the problem. In experimenting with seed of known provenance, results are thus often obtained which are poorer than ever known before; but nevertheless we carry on equally energetic work in order to realize something better.

Nature itself shows us hybrids, where the geographical ranges of two species meet. Thus SUKATSCHEW found hybrids between *Larix sibirica* Ledeb. and *L. Gmelini* (Rupr.) Gordon, where they meet around Lake Baikal. *Pinus nigra* Arnold crosses with *P. sylvestris* L., and *P. sylvestris* crosses with *P. mugo* Turra, where these tree-species meet in central Europe. In New Zealand we have obvious hybrid species at the natural regional limits between several species of *Nothofagus*—as, for example, *Nothofagus Solandri* × *truncata* and *N. Cliffordiana* × *fusca*.

R. G. BRETT has found hybrids in *Eucalyptus* in Tasmania, and that perhaps explains to some extent the very large number of species which have been described for that genus. As another example it may also be mentioned that in the Rocky Mountains, where the geographical ranges of *Picea sitchensis* Carr., *P. Engelmanni*, and *P. glauca* Voss. meet, there is no doubt of the existence of numerous hybrids—e.g. beside the forest-girdled Lake Louise.

As a special incentive to us Scandinavians we may recall our " thousand-year-old oaks ". These are the oldest living things in Denmark and very probably were growing while the Vikings sailed from our shores. Morphological studies make it probable, and cytological treatment provides evidence,

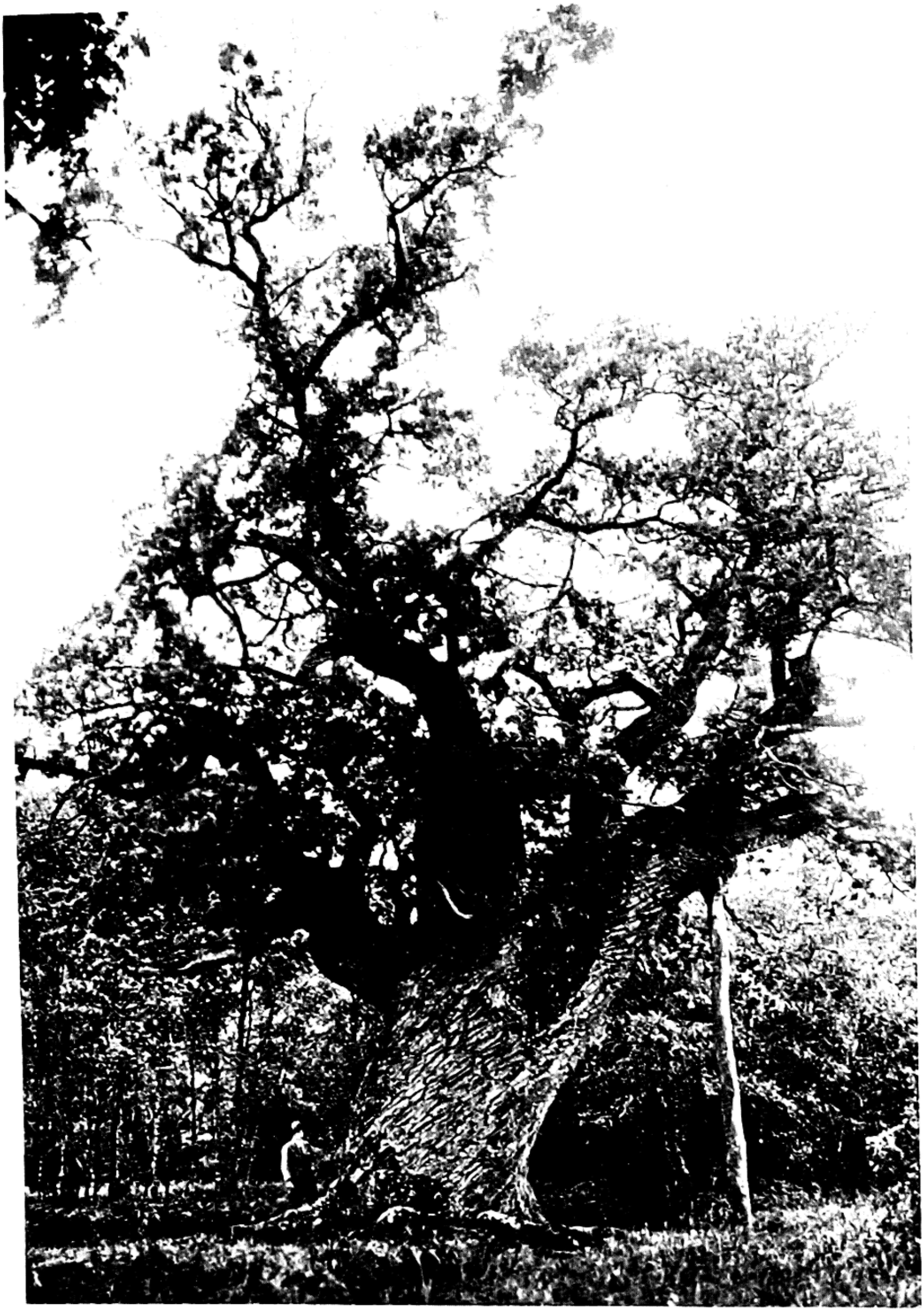


Fig. 50. One of the oldest trees in Denmark, an oak 800–900 years old, called "Snoegen" (the Twisted Oak). A hybrid between *Quercus robur* and *Q. petraea*.

that at least our most magnificent old oak " Snoegen " is of hybrid origin. It contains inherited tendencies from both *Quercus robur* and *Q. petraea.* With its healthy stem, which is 8·62 m. (84·4 ins. Q.G.) in circumference at 1·3 m. (4 ft. 3 ins.) above ground level, and a vigorous crown, it succeeds in conveying the impression of something " primaeval "—something still extremely powerful and vigorous, which it is undoubtedly desirable to imitate.

Since mankind by means of botanic gardens, by making use of rare and beautiful trees in parks and gardens, and later by the use of alien tree-species in forestry, has interfered in the natural distribution and got it thoroughly mixed up, it is not surprising that many more hybrids have arisen and have been described by the botanists.

For the further use of hybrids which have arisen spontaneously, and the importance which they have thereby achieved, their manner of reproduction has been of decisive significance; flowering conditions have also had an important effect. For a genus like *Populus*, especially the Tacamahaca and Aegeiros groups, with easy vegetative reproduction by cuttings and the pronounced diœcious distribution of their flowers, opportunities for the occurrence and use of hybrids have been unique. On the basis of crossings which have arisen spontaneously alone there are already in widespread cultivation a number of types (clones), certainly rather confusing to the taxonomist.

In the elm, plane, lime, and oak genera an equally important number of clones have been established by gardeners, and their existence can be explained only as being of hybrid origin. Among the elms we have the large group × *Ulmus hollandica* Mill. (*U. glabra Huds.* × *carpinifolia* Gleditsch), which includes, amongst others, the Huntingdon elm (*U. hollandica vegeta* (Loud.) Rehd., already known from about the middle of the eighteenth century. It has attained great popularity, especially in the south of England, as a valuable, vigorously growing park tree. Another much-used elm in this group is *U. hollandica belgica* (Burgsd.) Rehd., which has been specially employed in the planting of avenues on the continent of Europe.

The commonest plane in northern Europe is *Platanus acerifolia* (Ait.) Willd. (London plane). Along with several forms (clones) referred to as varieties of this, it is regarded as being the product of a cross between the two species occurring from southern Europe to western Asia and in North America, *P. orientalis* and *P. occidentalis* respectively. *P. acerifolia* is known only in cultivation, and it seems to have arisen before 1700. The majority of present-day cultivated planes are referred by the taxonomist to *P. acerifolia,* and various forms of it, and are assumed to be of hybrid origin. In cultivation it has become particularly widespread by reason of its capacity to grow in large towns.

Tilia europaea L. (*T. vulgaris* Hayne), park lime, common lime, is very widespread in Europe. Its origin is not known, but is most commonly taken to be as a hybrid between *T. cordata*. Mill. and *T. platyphyllos* Scop.

Better known are some examples from the genus *Quercus*, where there does not seem to be any doubt of their hybrid origin. *Quercus hispanica* Lam. is described as the hybrid *Q. cerris* L. × *suber* L., and is generally known in cultivation, while it occurs now and again between the parent species in southern Europe. Amongst the numerous products of crossing described as varieties, special mention may be made of *Q. hispanica Lucombeana* (Sweet) Rehd., which is stated to have originated spontaneously in an English nursery about 1765. There is mention of fertile hybrids, so that some of the types have perhaps also arisen from back crossings. Of the various forms (clones) there are several vigorously growing park trees, and special reference may be made to *Q. hispanica dentata* (Wats.) Rehd. (*Q. cerris* var. *fulhamensis* Loud., Fulham oak). This is of tall and vigorous growth with a markedly erect stem, and worthy of being considered in forestry. (See J. C. LOUDON: *Arboretum et Fruticetum Britannicum*, London, 1838, Vol. III, Figs. 1712 and 1713, showing the tree sown in the Exeter Nursery of LUCOMBE about 1762 from seed taken from *Q. cerris*.)

It was the value of the trees for parks and planting in avenues which induced gardeners to preserve individuals which had appeared spontaneously, by the methods of grafting and budding which are not specially difficult for these genera. But foresters did nothing—it was easy only for " green-fingered " gardeners to make use of these artifices. Nevertheless in this field, work of the greatest importance was carried out by gardeners. This demonstrated in the best possible manner how valuable material may be which arises through the occurrence and preservation by vegetative propagation of hybrids.

If we look well where we are going, and assume a forestry attitude to the results achieved, we shall find many fine tree-shows which demonstrate the peculiar features of individuals (clones). But we must not reproach gardeners and garden-lovers for laying stress almost entirely upon the need for discovering and making more use of ornamental features.

It is only our own fault that we have not taken part in this centuries-old task, and realized its value if it had been undertaken in the interests of forestry. But we should not despair; we should merely take a lesson from this, and see it in relation to our opportunities for combining it with the employment of seed-gardens. In that way we can utilize it without interfering seriously in a unilateral manner with " natural forest management ". The only thing that will appear to be exceptional is that we should use clones for direct planting in the forest. We should, on the other hand, use vegetative propagation in producing clones from selected trees, in order to bring them together in the proper manner in our seed-gardens, and provide seed to furnish hybrids with the best possible inherent tendencies.

Artificially produced hybrids of forest trees were mentioned for the first time by KLOTZSCH, who in 1845 carried out the following pollinations: *Pinus sylvestris* × *nigricans*, *Quercus robur* (probably *Q. robur* Mill., not L., i.e. *Q. petraea* Liebl.) × *pedunculata* (*Q. robur* L.), *Alnus glutinosa* × *incana*, and *Ulmus campestris* (*U. procera Salisb.*) × *effusa*. The seeds produced, as well as seeds from the parents, were sown on one and the same day alongside one another, with the result: " dass die Bastardbäume nach nunmehr 8 Jahren bestimmt um ein Drittheil stärker und grösser sind, als die Stameltern."

BURBANK was the first to begin experiments with artificial pollination of species of *Juglans*, when in 1877 he produced " The Royal Black Walnut ". This is generally spoken of as *J. nigra* × *californica*, but according to REHDER in 1947 is more correctly called *J. nigra* × *Hindsii*. This is said to have reached a height of 100 ft. in sixteen years, with a diameter of 3 ft. at 3 ft. above the ground. In spite of its strong growth, its timber is said to be exceedingly hard and close-grained, to take a silky polish, and to be superior even to ordinary black walnut lumber, more nearly resembling the tropical mahogany. Another of BURBANK's hybrids is " The Paradox Walnut ", which was produced in 1887 and which with the adopted nomenclature should be *J. Hindsii* × *regia*. In sixteen years it was 60 ft. high with a diameter of 25 ins. at 3 ft. above ground level.

The experiments in controlled crossing made by both KLOTZSCH and BURBANK are particularly promising. Nevertheless it must be said that they have not led to very appreciable results. KLOTZSCH's experiment has remained practically unheeded, which is certainly not the case with BURBANK's walnuts, which were highly commended, while at the same time attempts were made through nurseries to spread them by graftings. That the new trees, in spite of this, have not been more used, and in particular that there has been very little attempt at imitation, is due not so much to the fact that their value was doubted, but rather to the difficult method of propagation. Had it been possible to reproduce it by cuttings as easily as some of our commonest poplars, it is probable that from these and similar experiments generally known clones of practical importance would have arisen.

With practical results in mind work has thus mainly been confined to the poplars. Thus in 1912 HENRY produced the hybrid *Populus angulata* Ait. × *trichocarpa* Hook. and Gray. It is called *P. generosa* Henry, and was of extremely promising growth. In Europe it has unfortunately proved to be susceptible to rust, whereas it does much better in North America, where it was used for further improvement by SAX in the Arnold Arboretum. That is only one example from HENRY's work, which was later carried further in several places, amongst others in the U.S.A. by the Oxford Paper Co. in co-operation with the New York Botanical Garden; in Germany by W. v. WETTSTEIN; in Italy by PICCAROLO; in Canada by HEIMBURGER; in Sweden especially by H. JOHNSSON at Ekebo; and in Belgium by C. MUHLE LARSEN at the Institut de Populiculture at Grammont. This has mainly been done from a recognition of the practical importance of the work, which received special impetus after WETTSTEIN had shown how easily flower-bearing branches could be brought artificially in a greenhouse to continue normal fruit-setting, and could then be subjected much more easily to artificial pollination.

In the nearly related genus *Salix*, which likewise readily reproduces itself by cuttings, and most species of which quickly reach the flowering age, the work has not of course been so inviting for forestry practice, but it has been undertaken by HERIBERT: NILSSON from an experimental systematic point of view. Of the results obtained by HERIBERT: NILSSON, it will merely be noted here that his researches showed that the morphological specific characters described for such pronounced species as *Salix caprea* and *S. viminalis* are also subject to segregation according to MENDEL's laws.

Hybrids of pine, along with other problems within the genus *Pinus*, have also been the special object of work at the Institute of Forest Genetics at Placerville, California, being the " Eddy Tree Breeding Station " founded in 1925. Their oldest hybrid, *Pinus attenuata* × *radiata*, sown in 1929, attracted much attention. Because of the labour conditions in the economically difficult years, in spite of this satisfactory result of a hybrid produced under control, it was not followed by a second one until much later. After that the work grew rapidly, and at Placerville they are now engaged in a large-scale and promising task, which is also connected with that concerned with resistance in White pines mentioned in previous chapters.

In this connection it should also be mentioned that F. I. RIGHTER at Placerville has recommended the use of hybrids by employing seed of the F_1-generation without controlled pollination. In Scotland J. K. LEVEN, by using controlled pollination, re-tested the hybrid larch mentioned earlier in that connection and provided final evidence of its hybrid origin. (J. K. LEVEN: *Quarterly Journal of Forestry*, 1949.)

There is much to indicate that forest-tree breeding can derive great benefits from a use of hybrids. It would, however, be wise to mention a few older experiments, which are an invitation to show some caution in the choice of the initial material and in assessing the results achieved.

In a previous chapter (IV, p. 55) mention is made of an experiment of 1924 in crossing *Abies Lowiana* and *A. grandis*. This provided only nine plants, the largest of which was at an age of twenty-nine years, 20·6 m.

(67½ ft.) in height—a beautiful tree in vigorous growth. Similar fine trees have been produced in subsequent larger experiments. This is so far good, but the most interesting thing is the extraordinarily wide variation of the progeny, right from apparently pure *A. grandis* to bluish-grey *A. concolor*, but by far the greatest part are types varying between these two extremes. Although on the whole this has given a fairly good forestry result, yet we should first of all consider the botanical aspect of the matter.

Fig. 51. *Juglans*. Progeny from one tree in the same year; controlled and uncontrolled pollinations (1935). *Left: J. Sieboldiana* × *cinerea*. *Right: J. Sieboldiana*. Photographed on 2nd March 1951.

The progeny does not resemble the result of a species cross, but is much more reminiscent of a back cross. With the uncertainty which prevails about the correct interpretation of *A. Lowiana* as a species or as a variety of *A. concolor* or *A. grandis*, it must rather be regarded as a step towards an elucidation of this problem. Since the initial material was two trees which were introduced here as long ago as 1864, this is an example of how careful we should be with them in breeding work. It may also be put in this way, that we can expect, when we carry out controlled pollination in breeding, that we may chance to contribute to a revision of material which is now described as species and varieties.

Reference may also be made to an experiment with *Juglans Sieboldiana* × *cinerea*. This was made here with an isolated specimen of *J. Sieboldiana* Maxim. in our Forest Botanical Garden. Of a pollination in 1929 with pollen of *J. cinerea*, the largest plant at an age of twenty-four years was 16·5 m. (54 ft.). It gave early indications of a considerable heterosis, so the crossing was repeated on a larger scale in 1935. There were ninety-five plants, which at one year had a mean height of 45·1 cm., whereas one hundred and fifty plants of *J. Sieboldiana* from the same tree arising from free pollination had a mean height of only 38·4 cm. Both lots were planted out as one-year seedlings in two groups standing beside one another in our Arboretum, and the difference in growth has become even more striking with the years.

Plot	1949, 14 years old		1954, 19 years old	
	Mean Height	Mean Diameter	Mean Height	Mean Diameter
	m.	cm.	m.	cm.
Juglans Sieboldiana . .	7·03	8·31	9·03	12·88
Juglans Sieboldiana × *cinerea* .	10·45	12·21	12·31	17·63

There cannot be any doubt that the *Juglans Sieboldiana* × *cinerea* produced by controlled pollination is of far more vigorous growth than the *J. Sieboldiana* raised by free pollination. This provides further evidence of a successful result from a species cross, in that the hybrid—in addition to its thriving growth—also displays a nice uniformity. It would not be reasonable, however, to assume that the whole of the difference in growth between the two progenies is an expression of the hybrid-vigour attained in comparison with *J. Sieboldiana*. It is probable that the progeny of *J. Sieboldiana*, which was produced by free pollination on a single standing individual, may have been stamped by inbreeding depression.

We must pay attention to such a phenomenon, when we work with the otherwise very promising material which has been collected in botanic gardens and other similar institutions, by the old landed estates, by forest research stations, and so on. Provided we make it clear what we are working with, we may also in this way achieve results which may present special interest. It may not be merely a case of working with single standing individuals—there may also be trees which have themselves been bred from individuals placed in isolation in other botanical establishments, and produced from them by self-fertilization. They will be of great interest. In many cases we shall find crosses occurring in progeny of single isolated individuals; these crosses may be selected precisely because of their luxuriant development. This is a great incentive to search for the best historical information about old botanical gardens and tree stands in arboreta. The material we may find there is no less interesting than in the areas of untouched virgin forests. These are only two of the various items to which we must pay attention, in view of the various advantages we can derive from them.

From among the data we must, however, note what is actually known, and what are favourable or unfavourable assumptions. We must, above all, subject the material to a check by means of historical investigations, controlled pollination, and vegetative propagation. Only in this way can we know what may be read from the individual experiment. In addition we must have contact with dendrology in order to get the best possible information about the variation in the tree-species.

In recent years the hybrid *Populus tremula* × *tremuloides* (and its reverse) has attracted special interest. It was first mentioned by WETTSTEIN (W. v. WETTSTEIN: "Forstpflanzliche Züchtungsversuche," *Botaniska Notiser*, 1937), but it was rather remarkable during the blockade of the war years how it was quite intensively used on the basis of a very few individuals, which were found as rarities in Scandinavian botanical collections.

In Sweden they had two trees of *P. tremuloides* available, one of which was in the Gothenburg Botanical Garden and the other at Uppsala. They were both female trees, and the crossings were made between this female material and male trees of the *P. tremula* occurring naturally in Sweden and the types of the species raised at Ekebo. The first *P. tremuloides* × *tremula* was produced from this in 1939, and from 1940 further experiments were initiated. In 1941, in a private collection in Denmark (Knuthenborg Park) a tree of *P. tremuloides* was discovered, which like the two in Sweden was a female tree. In 1942 we produced from this our first *P. tremuloides* × *tremula* (S.676), and in 1943 the first lot of any size (S.707), a group of which, consisting of four hundred individuals, was planted at the Arboretum here and a similar one at the Hellestrup Poplar Research Station, in addition to small lots scattered over a large number of districts. From the three trees of *P. tremuloides* existing thus as " rarities " in Scandinavia, even under the barriers imposed by the war, widespread experiments were achieved which gave much information, so that immediately after the war ended we were ready to utilize the greater opportunities when we were able to import material from the natural stands.

In Sweden and Denmark the problem was attacked in rather different ways. Whereas in Sweden they proceeded more carefully with a large number of crossings in various combinations, including both diploid and tetraploid *P. tremula* (see chapter on " genetics "), and kept the work for quite a long time at the preliminary experimental stage, we in Denmark devoted ourselves more quickly but perhaps also more recklessly to an almost immediate commercial application of the first promising results.

The two different lines which have been taken may each have their own advantages, so that something good may be said on both sides. In Sweden they have more research material at their disposal, and that has been, amongst other things, the basis of the last very optimistic account from Ekebo. In this HELGE JOHNSSON has given a review of the growth in youth of the hybrid aspen, and what he himself calls a " future prognosis " of the future economic yield. (HELGE JOHNSSON: *Föreningen för växtförädling av skogsträd*: Annual report, 1952). From this (p. 37) may be quoted:

	Age	No. of Stems per ha.	Height m.	Diam. cm.	Volume of Mean Tree	Volume per ha.
Hybrid aspen	32	390	23·7	28·5	0·7950	310·1
Sätra aspen .	60	398	24·0	28·5	0·7234	288·1

(Sätra aspen represents one of Sweden's very best occurrences of *P. tremula*.)

The figures for the Sätra aspen (*P. tremula*) are based on an old stand, in which a sample-plot has been measured, whereas the figures for the hybrid aspen are calculated from original data from a young plantation of triploid hybrid aspen in a so-called " short-term experiment " at Ekebo. This little plantation covers an area of 12·5 m.^{2} (15 sq. yds.), replicated three times and originally with twenty-five plants in each lot. It was planted in 1945 with one-year plants and has been thinned annually since 1948. When the calculations were made there were 17 trees left of hybrid aspen, and JOHNSSON himself draws attention to the criticism which can thus be directed against such calculations.

As an advantage of hybrid aspen he draws special attention to the great difference in the rotations in the calculation, and also to a relatively slight but distinct improvement, which is secured by using tetraploid *P. tremula* instead of the ordinary diploid. The overwhelming effect of *P. tremuloides* when crossed with *P. tremula* is explained by the resistance of the hybrid to rust (*Melampsora* sp.) and aspen scab (*Fusicladium radiosum*) brought to it from *P. tremuloides*, and he refers to an experiment some years old with seedlings of *P. tremuloides* which have given a vigorous growth in youth similar to that of hybrid aspen.

When we in Denmark devoted ourselves to such a speedy—and it is willingly conceded rather rash—seed-production of hybrid aspen on a large scale for use in practical forestry, the immediate reason for this was the favourable growth in youth which can be very easily demonstrated, and also the easily observed resistance of the hybrid to rust and scab, which in this country at once checked and in the course of a few years almost exterminated the pure *P. tremula* in the first comparative experiments with hybrid aspen and *P. tremula* of Danish origin. Add to this a general impression of *P. tremuloides* as a more shade-bearing tree than *P. tremula*, so that the hybrids might be expected to be better adapted to utilize the ground. Lastly, add to this the opinion we held that if the hybrid and the cultivation of aspen in general were to have any significance in our silviculture, we must in conjunction with continued experiments also use it as soon as possible under different conditions in our forestry, of which so far we really had no experience. By presenting the advantages and difficulties of the problem and by a happy relationship between our research station and practical silviculture, this rapid development has succeeded. It has been valuable, as the experience to date supports the earliest experience and gives us a belief that through the hybrid aspen we have obtained a valuable tree for our forests.

A plantation of 1944 with one-year plants, four hundred of which were put out at 2 × 2 m. (6½ × 6½ ft.), contained in the spring of 1954—after various thinnings—the following:

S.707: Sown in 1943, planted in 1944, area 1,600 m.^{2} (1913 sq. yds.), age ten years: height 10·6 m. (34·8 ft.), diam. 10·1 cm. 4·0 ins.).

A simultaneous planting of the same seed-lot at Hellestrup, in which were planted five hundred plants at a spacing of 1·5 × 2·0 m. (5 × 6½ ft.), with the same number of alder (*A. cordata*) in admixture, has given the following results:

S.707: Sown in 1943, planted in 1944, area 1500 m.^{2} (1615 sq. yds.), age ten years: height 12·3 m. (40·4 ft.), diam. 10·4 cm. (4·1 ins.).

The largest plant, 14·5 m. (47·6 ft.), diam. 15·5 cm. (6·1 ins.).

Alongside the area of hybrid aspen planted in the Arboretum and mentioned above there were planted at the same time a number of *P. tremula* which had a common father with the hybrid aspen used, but the pure *P. tremula* was here so soon and strongly ravaged by rust and scab that the majority succumbed, or remained so small that no comparison could be made. At Hellestrup a similar comparative lot of *P. tremula* is more healthy; its mean height is 6·7 m. (22·0 ft.), and its largest plant has a height of 8·8 m. (28·8 ft.), and also a timber production which is negligible in comparison with the hybrid aspen. The father used was the ordinary diploid Danish aspen.

From plantations in commercial forestry an example from Falster State Forest district may be quoted. The aggregate area is 1·17 ha. (2·90 ac.), where in 1947 there were planted hybrid aspens at 1·5 × 2·0 m. (5 × 6½ ft.). After a number of fellings the measurements now are:

S.87 and S.91: Sown in 1946, age nine years: height 8·8 m. (28·8 ft.), diam. 7·8 cm. (3·1 ins.).

Since the spring of 1946 pollen has been imported from Canada; new material of *P. tremuloides* both as seed and as clones has also been introduced from selected trees in Canada. As in Sweden, we have in this material found a strikingly vigorous growth in the case of the *P. tremuloides* imported as seed, in which, however, we also think that we have observed a not inconsiderable variation. Of the crosses made in Denmark the most promising so far seems to be the hybrid between *P. tremula* from Poland and *P. tremuloides* from the district around Vancouver, B.C., raised with material from populations cultivated in this country.

If we revert to the very numerous hybrids of poplar in the Tacamahaca and Aegeiros groups (p. 147), it must not be overlooked that the results so far achieved with them were to an overwhelming degree attained by hybrid formation between a few individuals (clones) of the individual species cultivated in plantations. It should be possible to expect other results from a further choice of trees for breeding in populations of the species, whether one wishes to make such a choice in the natural range of the species, or on the basis of gathered seed, which is brought to the stage of populations in the climatic region set aside for the breeding. For that reason alone it will be of great value to make population studies in the genus *Populus*, such as the one initiated by SCOTT PAULEY at Harvard Forest in Massachusetts.

Whether there is now a special opportunity for spontaneous occurrence of hybrids, where an exotic species is cultivated in the form of a few specimens, or whether there are botanical collections which call for experiments with controlled pollinations, it must not be forgotten that that is only the first step on the path of progress. The work must be taken farther in an intensive study of the variation in individual species in order to discover the best possible combination of individuals.

We must not give in, but be prepared to undertake a great deal of work in this field, for we must remember that as soon as we have found the right material for the production of a hybrid, we have very special opportunities for its further utilization.

CHAPTER X

GENETICS

IMPORTANT work can be carried out in forest-tree breeding even with quite a small amount of knowledge of the fundamental genetics. This may be likened to the fact that it is not research workers alone, equipped technically and scientifically, who have done the pioneering work in agriculture so far as the breeding of both domestic animals and agricultural plants is concerned. Much of the work has been based upon the skilled farmer's knowledge of his material combined with a direct assessment of the practical value of its varied qualities.

In the same way as agricultural development in this field has been favoured by close co-operation between the professional practitioners and all sections of research workers on the path towards purely scientific considerations, it will also be of decisive importance to forestry development that there should be a similar co-ordination between the different technical branches of forestry. It is very easy for forestry and industry to resign themselves complacently to finding some people with microscopes and typewriters in order " to look after " breeding, so that they can keep their conscience in order and safely cut their losses. This is on a par with men who have an interest in forest botany and improvement regarding it as their first duty to declaim against the destruction of the great wealth bequeathed to us in the natural growing-stocks spared by previous generations. Such consideration is merely superficial, and a particularly important task remains to be done in forging a chain of professions and interests which will unite all sections in a mutual understanding and a well-conceived plan for building up the forestry of the future.

The statement that important work can be carried out in forest-tree breeding, even on the basis of quite a small knowledge of fundamental genetics, should therefore be taken to mean that foresters working in practice can directly take up much of the work described above. This should on no account be taken as an invitation to halt at that stage; there are plenty of opportunities for making further progress.

All our tasks are not the same, however, but there are so many links to be filled in in the chain, which has to be forged in respect of forest genetics and forest-tree breeding in order to unite genetics and silviculture, that one has only to work independently on some of them in order to find and fill in the link which suits one best.

Foresters are not all alike. We differ as do the trees in a forest association. Just in the same way as trees, we are living beings whose behaviour is determined by a distinctive *heredity* and by the *external factors*, which have given us different habits and different opportunities for our work. Our person, like the " value " of a tree and, moreover, like the appearance of every other living thing, is determined not merely by what has been inherited from our forebears. What we have obtained as a gift in our cradle, when we were born, is our " predisposition ", our *genotype*, whereas the person developed later has an " individual stamp " which is called our *phenotype*.

The phenotype is the response of the genotype to the given external conditions, or it may be very concisely expressed as *phenotype = genotype + the external conditions*. It is extremely important to grasp this. Its recognition was one of the great advances in genetical research.

With an identical genotype, individuals will develop differently under different external conditions. We can see this most easily from a poplar, which is usually reproduced by cuttings from an originally single individual (a clone). When the cutting is set under the same conditions as the tree from which the cutting was taken, it has the same development. It was perhaps a large and beautiful tree in a well-sheltered botanical garden; but we do not get the same result if the cutting is put out on a barren heath or high up on a mountain under harsher conditions. If it should happen to live at all, it becomes perhaps only a stunted bush. From the genetical viewpoint, on the other hand, it does not suffer any " harm ". We obtain evidence of this by again taking a cutting from the stunted plant and transporting it back under the original good conditions, where it will grow up as a large and beautiful poplar like the original tree. Such a change, which is induced by external conditions and not by heredity, is called a *modification*. In this connection it is important to remember, however, that different genotypes can have different capacities for adaptation to change of environment, and these differences in capacity for adaptation (modification) are hereditarily determined.

Moreover, we must maintain that our " heredity ", or, if you like, the genotype of the tree, is alone determined by the inherent tendencies received from the parents. The genotype of the tree, which is embedded in the seed, is a product of the inherent tendencies received from the female and male elements, the ovule of the female flowers and the pollen of the male flowers.

In the case of human beings, where there is more certainty about mother and father, we observe at once, however, that all the children of the marriage are not identical. Although they have the same mother and the same father, yet the progeny do not possess an equal admixture of the inherent tendencies. They possess only some of the combinations of the inherent tendencies from the mother and the father. They are of different genotypes. A *combination* of tendencies takes place, and the variation appearing in the progeny has been found to follow definite laws.

GREGOR MENDEL was the founder of genetics by proving and discovering by controlled crossings the rules for segregation. These have received the name of the *Mendelian segregation laws*. MENDEL's fundamental research was carried out in the years 1857–1864, and the most important part of it was published in 1865; but in a remarkable way it remained unheeded up to about 1900, when his laws were again proved at three places each independent of the others. This rediscovery of the behaviour of heredity according to regular rules was at once followed up and expanded into what is now the extensive subject of genetics.

Genes and the laws of their inheritance had been discovered. The aggregate of the innate tendencies constitutes the genotype, whereas the single inherent tendencies are called genes. The name gene was originally introduced by W. JOHANNSEN as a symbol, an abstract term for an assumed unit of heredity, which later proved to be something very real. If the gene denotes essential differences such as difference in the colour of a flower or a markedly divergent growth-form of a tree, such as the pyramidal form of the oak (*Quercus robur* var. *fastigiata*), we speak of *qualitative* genes, which are mainly insensitive to the external conditions. If it is a question of less sharp transitions as, for example, the greater or less vigorous height-growth of trees, where it is more a matter of degrees of difference, the term *quantitative* characters is used, and these are mainly responsive to the external conditions.

Genes are not attributes in themselves, but they are inherent tendencies in respect of the attributes which have developed in the individuals. The (diploid) individual formed by fertilization has two genes occurring together as a pair for each attribute. If the individuals have two identical genes for the attribute in question, this is indicated by saying that they are characterized by identical twin tendencies, or by using the word *homozygotic*. If they have two genes which are opposite to one another (alternatives), they are said to be *heterozygotic*. Of the two genes opposed to one another, one is dominant (dominating), whereas the other is dominated (recessive). In genetics the genes are represented by letters of the alphabet, in such a way that dominant genes are shown with capital letters, whereas the corresponding recessive genes are shown with the same small letters. AA and aa are thus each by themselves homozygotic, whereas Aa is heterozygotic, and these are the only three possibilities in the (diploid) individual produced by fertilization. Only in the sex-cells occur either A or a. In the same way occur B and b, C and c, or any other genes. They can therefore be recorded as mathematical quantities and built up into formulae and diagrams.

The aggregate genotype is also constant in the sense that the modification brought about by the environment is not handed down, so that the gene is not affected by fluctuating external conditions. Another point to be noted is that there may be an abrupt change of the genes, which is called *mutation*. In recent times it has come to be regarded as a basic feature of every gene that it has the capacity to mutate and that the primary inherent variation arises by mutation.

It is not to be understood by this that all the genes of the genotype, or even the greater number of them, rather easily take to mutating. It happens only in the case of the individual gene, and then very seldom. It occurs spontaneously, as an exception, but it can also be induced both by physical (radiation) and by chemical action. In all cases, however, it has not been possible to prove that there is any conventional behaviour.

The mutation may take place in the sex-cells, so that the whole of the individuals which have arisen from them are affected by it, or it may arise in a part of the vegetative tissue, so that only the part which has developed from that tissue is affected by the mutation. Should the mutation occur in the sex-cells, not only will the whole of the plants derived from these cells carry its effects, but the attributes which have made their appearance (the genes altered by the mutation) will also prove to be hereditary when the seed is sown. In those cases where it is only a question of a change in a part of the vegetative tissue of the plant (e.g. a branch), the mutation can be perpetuated by vegetative reproduction from the mutated tissue. In horticulture, bud mutations are called " sports ", and they have provided opportunities to cultivate various garden forms of herbaceous plants and perennial herbs. For the ornamenting of gardens and parks certain mutations of the forest trees have received attention, such as weeping ash, snake spruce, fern-leaved beech, red-leaved oak, etc. These are mutations which have been preserved by grafting.

Although it is most frequently a case of getting something poorer, it has nevertheless been possible, both in horticulture and in agriculture, to make considerable progress in improvement by the use of mutations. As examples mention may be made of the sweet lupin in agriculture and the splendid flowering *Lathyrus* in gardening.

It must be admitted that mutations occurring spontaneously are rare, although there are great differences in their occurrence in the various plant species, and the relative amount of their frequency displays much variation. On the other hand, it is generally recognized that the mutation frequency may be increased to an extraordinary degree in an experimental way. What significance this may have for plant-breeding in forestry has still to be determined. That can only be decided by research, but the problem is such that it must be followed attentively.

A special kind of mutation is a doubling of the chromosomes, which has occupied a prominent place in the forest genetics of the present day, and will be dealt with later.

For the moment, however, it is not proposed to go further into general genetical considerations. According to the way the genes behave they are spoken of as complementary genes, polymeric genes, lethal genes, sterility genes, inhibiting genes, genes which couple, and many more, and their behaviour is so diversified that no attempt shall be made here to give any further description of it. For a more detailed genetical foundation reference should be made to pure genetics. Too brief an examination might lead one to believe that it was sufficient for an understanding of the multiplicity of cases which may arise in the genetical exploration of certain material. Nor should we stop at that. Foresters should not be geneticists—and geneticists should not be foresters. On the other hand we should try to understand one another, and what has been said can, I think, assist foresters part of the way to a genetical comprehension of the problems. Some of the foregoing chapters are more to be regarded as a forester's treatment of general botanical, genetical, plant-pathological, plant-physiological—or if you like, biological—questions for mutual consideration, and, I hope, for use in further co-operation.

We must, however, also bring in a word or two about *cytology*, which has become an important auxiliary science to genetics and has done good work by directing a great deal of attention to forest genetics and forest-tree breeding. NILSSON-EHLE's discovery of the triploid aspen in Sweden in 1935 was the direct cause of the founding of the " Föreningen för växtförädling av skogsträd ", which in the course of a few years has grown to be a very important institution. Largely on account of its cytological work it has become of consequence far beyond the frontiers of Sweden. The work on chromosomes and principally on the " doubling of chromosomes " was particularly such as to attract attention and inspire hope of rapid progress.

Trees, just like humans, and indeed all animals and plants, are built up of living cells. Study of cells is known as cytology, and as the cells contain the genes (the inherent tendencies), cytology is of the greatest importance for an understanding of the genetical problems.

The living cell contains a cell nucleus, which is in a position to divide as one link in the division of the cell. The division of the nucleus starts off with a gathering together out of its content of chromatin granules of a certain number of stainable bodies, which are called chromosomes. After appropriate preparation these can be observed under the microscope, and their number is characteristic of the individual species. The division continues with each chromosome splitting up in accordance with a cleavage procedure already fixed from the start, and each set of halves is drawn towards its own pole of the cell. They then break apart into two independent cells. Some part of heredity can be carried on through the other constituents of the cells, but, looked at as a whole, the chromosomes are the inheritance-bearing elements. They contain the genes, which occupy their places in the chromosome like pearls on a string. The chromosome at first it shaped like a thin thread, but later during the division of the cell it becomes short and thick, so that it practically assumes the form of a short rod. After the division of the cell the chromosomes undergo the same change, but in the opposite order, so that there is once more a cell with a content of chromatin granules.

Vegetative cells contain a double set of chromosomes and are called diploids, whereas the single set is normally found only in the sex-cells. At the formation of the sex-cells a reduction of the chromosome number to half takes place through a special mechanism which is known as the reduction-division. The number is doubled again on fertilization. The single set of chromosomes is called the haploid number, whereas the double one is called the diploid.

Triploid plants with three sets of chromosomes in the vegetative cells may arise by exceptionally formed diploid sex-cells fusing with a normal haploid sex-cell. *Tetraploid* plants with four chromosome sets in the vegetative cells may arise from two diploid sex-cells or by the fusing together of the cell nuclei in the vegetative (diploid) tissue.

As already mentioned, interest in forestry circles was drawn to these phenomena by NILSSON-EHLE's discovery of the triploid aspen, *Populus tremula* f. *gigas* (H. NILSSON-EHLE: "Uber eine in der Natur gefundene Gigasform von *Populus tremula*," *Hereditas*, 1936). It was found as a clone of considerable extent and is distinguished from the surrounding normal diploid aspen by having unusually large leaves, larger stomata, and stronger growth—very soon after were found several similar examples of triploid aspen which had arisen spontaneously, and which from the special capacity of the species to spread itself in clones by suckering had succeeded in forming stands of varying sizes. It may be particularly mentioned that two sample-plots situated near to one another, which were subjected to measurements by the State Forest Research Institute, happened to contain triploid and diploid aspen respectively. The stands were of the same age, which, from an assessment made in 1944, was estimated to be fifty-six or fifty-seven years. The triploid aspen was 11 per cent. taller, 10 per cent. larger in diameter, and the volume was 36 per cent. higher than the diploid aspen. It was also shown by other observations that the growth of the triploid plants was greatly superior.

This is in harmony with the fact that a stronger vegetative development in triploid plants is also well known from numerous examples of herbaceous plants. Because the triploid plants contain an unequal number of chromosome sets they are not fit for further reproduction by sexual means. On the other hand, by the crossing of triploid and diploid plants there is an opportunity now and then of producing tetraploid plants. The triploids can then be produced in quantity by crossing between tetraploid and diploid plants. On the basis of the triploid aspen discovered in 1935, which was crossed with normal diploid plants, as early as three years later a report was issued of the discovery of the first tetraploid plant. (H. NILSSON-EHLE: "Framstälning av skogsträd med ökat kromosomtal och virkesproduktion," *Sv. Papperstidn*, 1938.)

Chromosome duplication induced experimentally has been known for over forty years, but it was not until the action of the poisonous substance colchicine had been demonstrated, at the beginning of the 'thirties, that a rapid development in this field was brought about. Colchicine has been of very great importance indeed in the production of plants with doubled chromosomes. Although many of the plants produced later proved to be only partially doubled, the method is so convenient that by its means "doubled" species and species hybrids have been produced by hundreds in the plant kingdom. (O. J. EIGSTI: *Literature on Colchicine*, Evanston, Illinois, 1946.)

By the employment of colchicine early success was also achieved in Sweden in the production of considerable numbers of tetraploid aspen, as a first step to the use of the method on forest trees (H. JOHNSSON and C. EKLUNDH: "Colchicinbehandling som metod vid väkstförädling av lövträd," *Sv. Papperstidn*, 1940). Later, triploid *Betula verrucosa* was also found in Sweden, and by crossing it with diploid plants the coveted tetraploid plants were produced. It was also produced direct with the help of colchicine. Thus the same progress as with the aspen was obtained in this genus. Moreover, they are now working at Ekebo with both triploid and tetraploid plants of *Ulmus* and *Alnus*, amongst which one lot of triploid *Alnus glutinosa* (pollination between tetraploid and diploid) is described as unusually promising. It should further be mentioned that in Sweden they have also discovered natural tetraploids of *Picea Abies*. Extremely fine work has thus been done in this field in Sweden, and its great significance lies in the fact that it was so thoroughly and early taken up in connection with forest genetics.

If the results are looked at in relation to the cytological investigations undertaken into forest trees in other places, they give additional cause for optimism. Particularly through work which has been done in the U.S.A., one gets an impression of considerable variation in chromosome number within species and between species, which increases one's hope of favourable results from operations along experimental lines.

As early as 1929, R. H. WOODWORTH reported the discovery of tetraploid *Alnus glutinosa* and *A. japonica*, while WETZEL at the same time had determined the diploid number. Later, JONATHAN W. WRIGHT, in a work on

" Genotypic Variation in White Ash " (*Journal of Forestry*, 1944), found both tetraploid and hexaploid plants besides the most common diploid *Fraxinus americana*. This is noteworthy, especially as WRIGHT, when working simultaneously with *Fr. pennsylvanica*, found in it only diploid plants. Both studies were carried out in connection with an important experiment concerned with progeny from widely separated localities and displaying differences in ecotypes. From its whole nature and close resemblance to a forestry trial on the basis of seed collected in nature, WRIGHT's researches are particularly interesting. However, as WRIGHT concludes in his work on " Ecotypic Differentiation in Red Ash " (*Journal of Forestry*, 1944): " If closely related species in other genera are as distinctive in their genetic make-up as are these two (*Fr. americana* and *Fr. pennsylvanica*), there is much work ahead before accurate generalizations can be made."

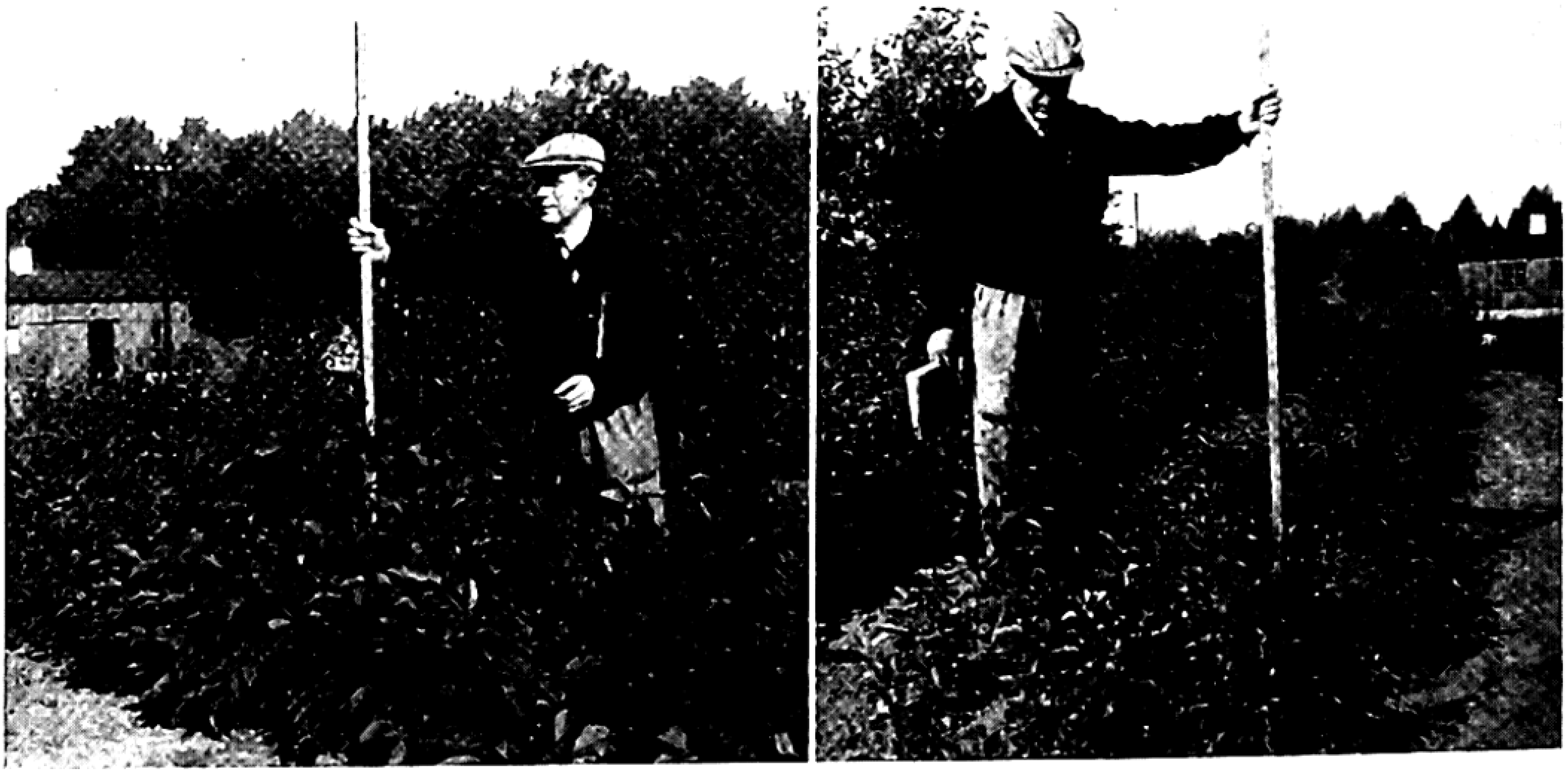


Fig. 52. *Alnus*. Progeny from one tree in the same year; controlled and uncontrolled pollinations. Two-year-old transplants (1/1). *Left:* Triploid plants, *Alnus cordata* (diploid) × *A. subcordata* (tetraploid). *Right: A. cordata* from seed resulting from free pollination. Photographed on 20th September 1941.

Forestry is making only its first contact with the problems, which must be taken up by co-operation between forestry and botany. As is only natural, the work is being taken up from the botanical viewpoint, but it is important that forestry should support it in full measure in order to be ready to utilize its results.

In Denmark, with its small geographical extent and its almost complete lack of untouched forest, we have not had much opportunity to search for forest trees with different chromosome numbers as evidence of a natural variation. However, as early as 1925, HELMS and JØRGENSEN had described a triploid hybrid between *Betula pubescens* and *B. verrucosa*, found in nature (A. Helms and C. A. Jørgensen: "Birkene paa Maglemose," *Dansk Bot. Tidsskr.*, 1925). Moreover, we have been modest in our work with colchicine, which has been used with such great success in Swedish forest genetics. In cytological work with forest trees we have mainly concentrated upon investigations based on our collections of trees in arboreta. This should be mentioned as an example of how, because of the small amount of information there is regarding our forest trees, it can also be of value to use such material as a starting-point. There remains the very material question of trees with unusual chromosome numbers as the result of hybrid formation or of trees of unknown origin.

From a forestry experiment with seed, which was collected from an *Alnus subcordata* in the Forest Botanical Garden, the result was so promising that it resulted in a request for further research with this tree-species (*Det Forstl. Forsøgsv.*, 1926, p. 356). By cytological examination it was later proved that the *Alnus subcordata* used was tetraploid, and that the progeny consisted almost exclusively of triploid plants, which had arisen by fertilization from surrounding diploid plants of closely related species. Morphological investigations gave as their result that the fertilization must to an overwhelming extent be presumed to have been done by diploid *Alnus incana*. The tetraploid *Alnus subcordata* was not by any means of imposing growth, but, on the other hand, the triploid progeny was of pronounced vigour of growth. One triploid plant, which is thought to have been produced by pollination by *Alnus incana*, has now at twenty-seven years of age a height of 21·1 m. (69 ft.) and a diameter of 60 cm. (23¼ ins.), and still seems to be growing strongly.

The causes of the vigorous growth can only be guessed at. It might be attributed to the triploid nature of the progeny, but with equal reason it might be taken to be an expression of heterosis. The opportunity did not

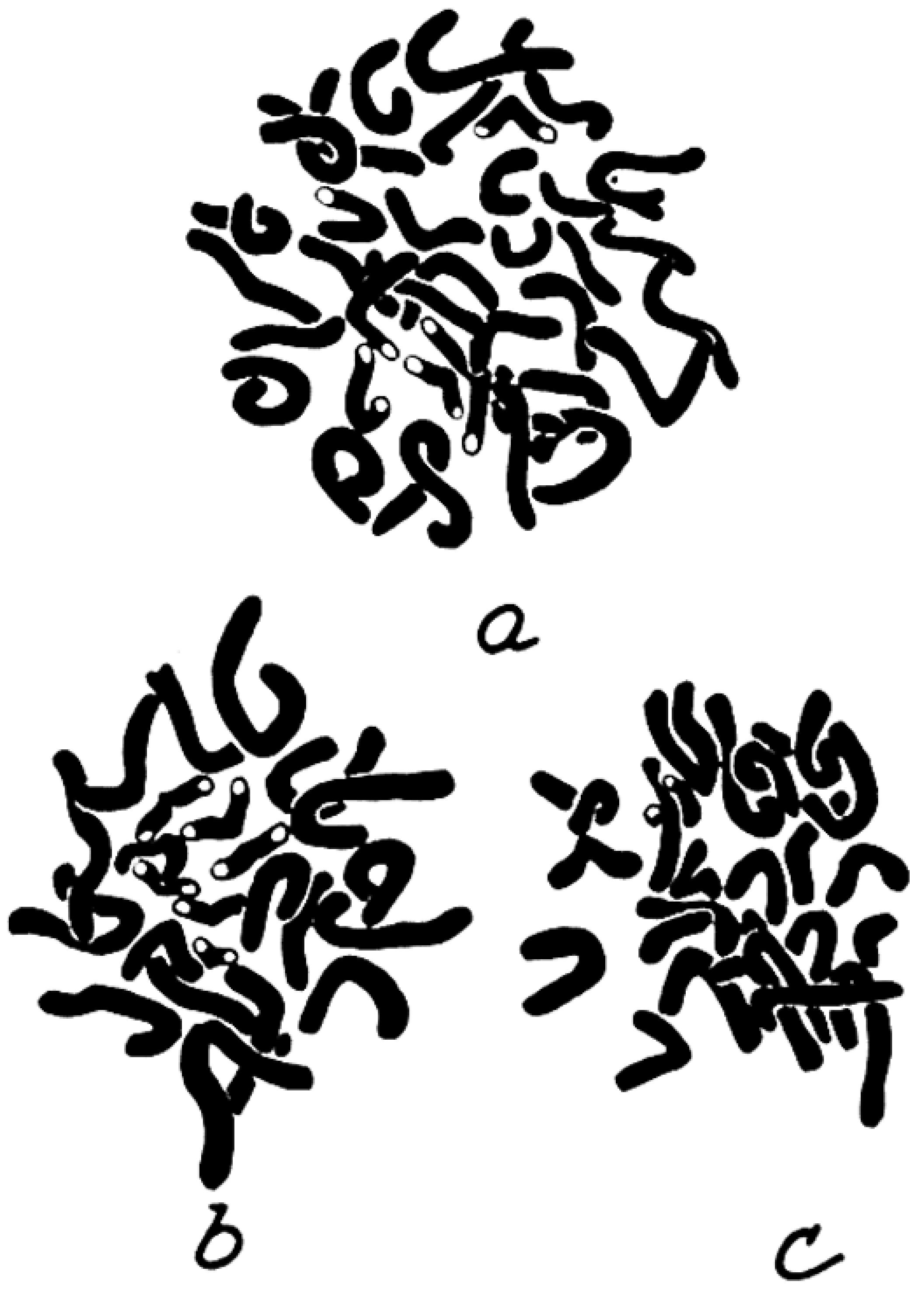


Fig. 53. Chromosomes of diploid and triploid larches. Somatic metaphase. (a) *L. decidua* × *L. occidentalis*, 2n = 36. (b) *L. decidua*, 2n = 24. (c) L. *occidentalis*, 2n = 24. All three figures magnified about 1,500 times. From C. Syrach Larsen & M. Westergaard in the Journal of Genetics, Vol. 36, p. 525.

present itself of throwing more light on the origin of the tetraploid *Alnus subcordata*. It was planted in 1864 and was found to be " completely identical with the type specimen ", which was the substance of the description given of it by C. A. MEYER. (K. GRAM and others: *Contribution to the Cytogenetics of Forest Trees, II, Alnus Studies*, 1941.)

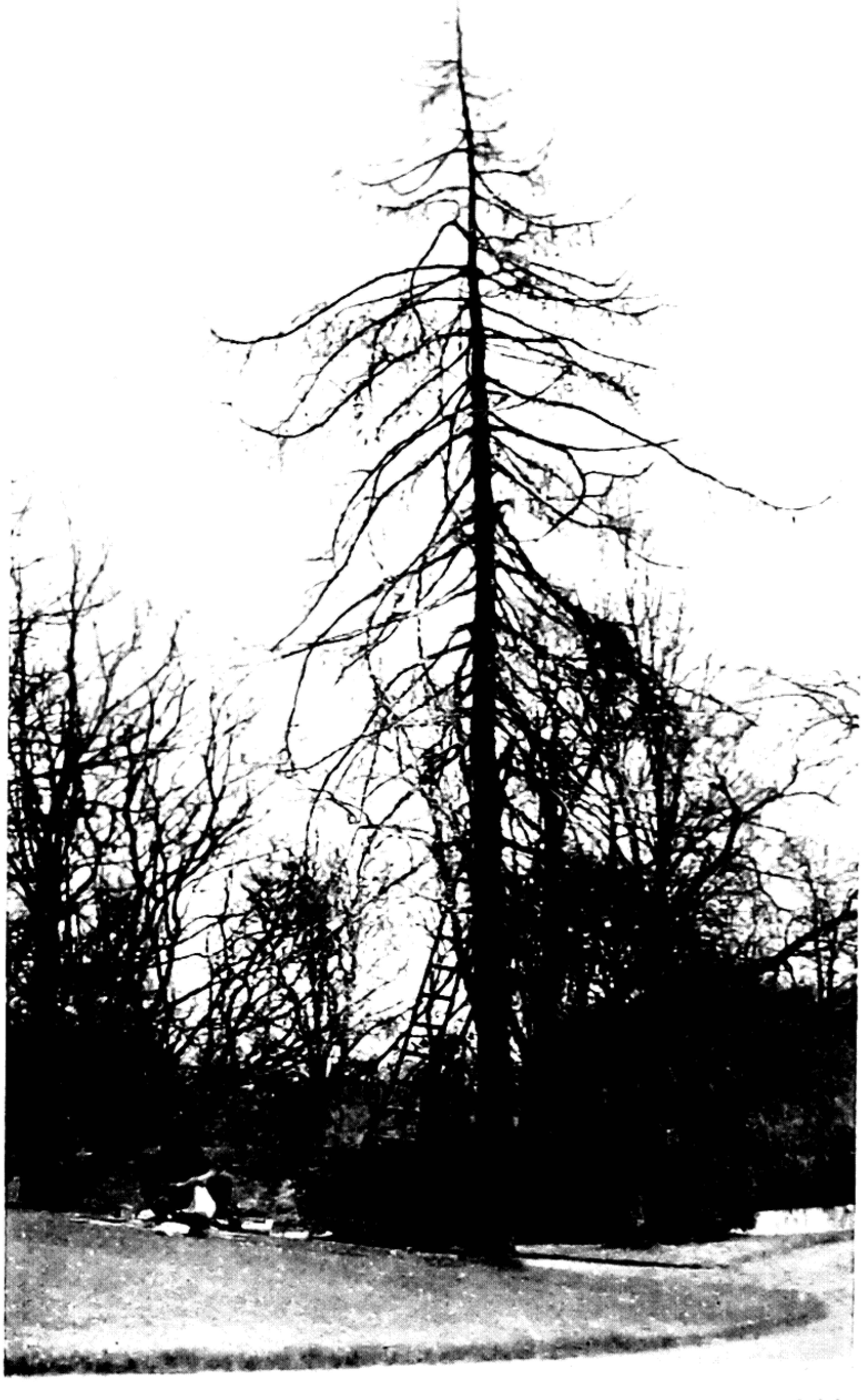


Fig. 54. Tetraploid *Larix decidua* in the park at Gisselfeld, Denmark, Photographed in 1949.

In 1930 a controlled pollination of *Larix decidua* was made with pollen from *L. occidentalis*. This gave the surprising result that from 534 seeds only one plant was produced, which in its first year was already 27 cm. (10·8 ins.) high and was extraordinarily robust. It flowered for the first time in the Arboretum in the spring of 1938, turned out to be triploid, and must be presumed to have arisen by the union of a normal ovule of *L. decidua* with a diploid (unreduced) male cell from *L. occidentalis*. This was all the more astonishing, as the diploid chromosome number ($2n = 24$) had previously been the only one known in *Larix* and a number of closely related genera of conifers.

In the hope of raising through this triploid plant a tetraploid larch, quite a number of crossings have been made between triploid and diploid plants. Although quite a number of plants have been obtained, there has still been no success in arriving at the tetraploid in that way. By a stroke of luck the first known tetraploid plant of larch was found in quite a different way, and it was not a young plant but a considerable tree. This was in 1949, and its age was presumed to be fifty-six to fifty-eight years Its height was 15·2 m. (49·9 ft.), its girth at 1·3 m., 97·5 cm. (9·6 ins. Q.G.).

It was both found and examined cytologically by H. CHRISTIANSEN (" A Tetraploid *Larix decidua* Miller," *Det Kgl. Danske Vidensk. Selskab., Biol. Medl.*, Vol. XVIII, No. 9, 1950). The tree stands in a private Danish arboretum, at Gisselfeld Castle, but there is a distinct probability that it was introduced as a variety under the name of *L. decidua* var. *pendula* from an English nursery.

It was also by " an accident " that NILSSON-EHLE came across the first triploid *Populus tremula*, which gave such a vital impulse to Swedish genetics. If we look at this in connection with the American and other investigations into cytological conditions in forest trees in their natural habitat, and think of the short period of years of deliberately planned work in this field, there are reasons for expecting a steady and even greater advance in cytological work in support of forest-tree breeding.

On the other hand, there is no doubt that for a time it was expected that there would be more rapid progress in plant-breeding as a whole on the basis of plants with increased chromosome number. Although remarkable results of practical importance were achieved in the case of herbaceous plants, yet these also took a longer time than had been expected. This applies also to forest-tree breeding. It is, in the first place, by making possible new genetical combinations as a basis for continued selection work that the increased chromosome number seems to have significance. It must not be overlooked, however, that in forestry we have special advantages due to easy vegetative propagation, and can in that way have an advantage over breeding from herbaceous plants. A tetraploid plant, which is inherently weak, but has been found to furnish valuable triploid plants through diploid pollination, can quite conceivably be turned to account by grafting, in a seed-garden established for that purpose, in the same way as is done for the production and use of hybrids.

If it is desired to make a comparison between the possibilities of reaching economically important results by using hybrids, with attempting to do so by a use of plants with increased chromosome number, it would not be wise to express an opinion in advance on these rather distant possibilities. In this, as in so many fields, it is not wise to take either one path or the other; the wisest thing to do is to keep one's eyes open for possible advances along both lines. There are valuable triploids in pure species, but there are also many examples of fine results of species crosses with no change in the normal

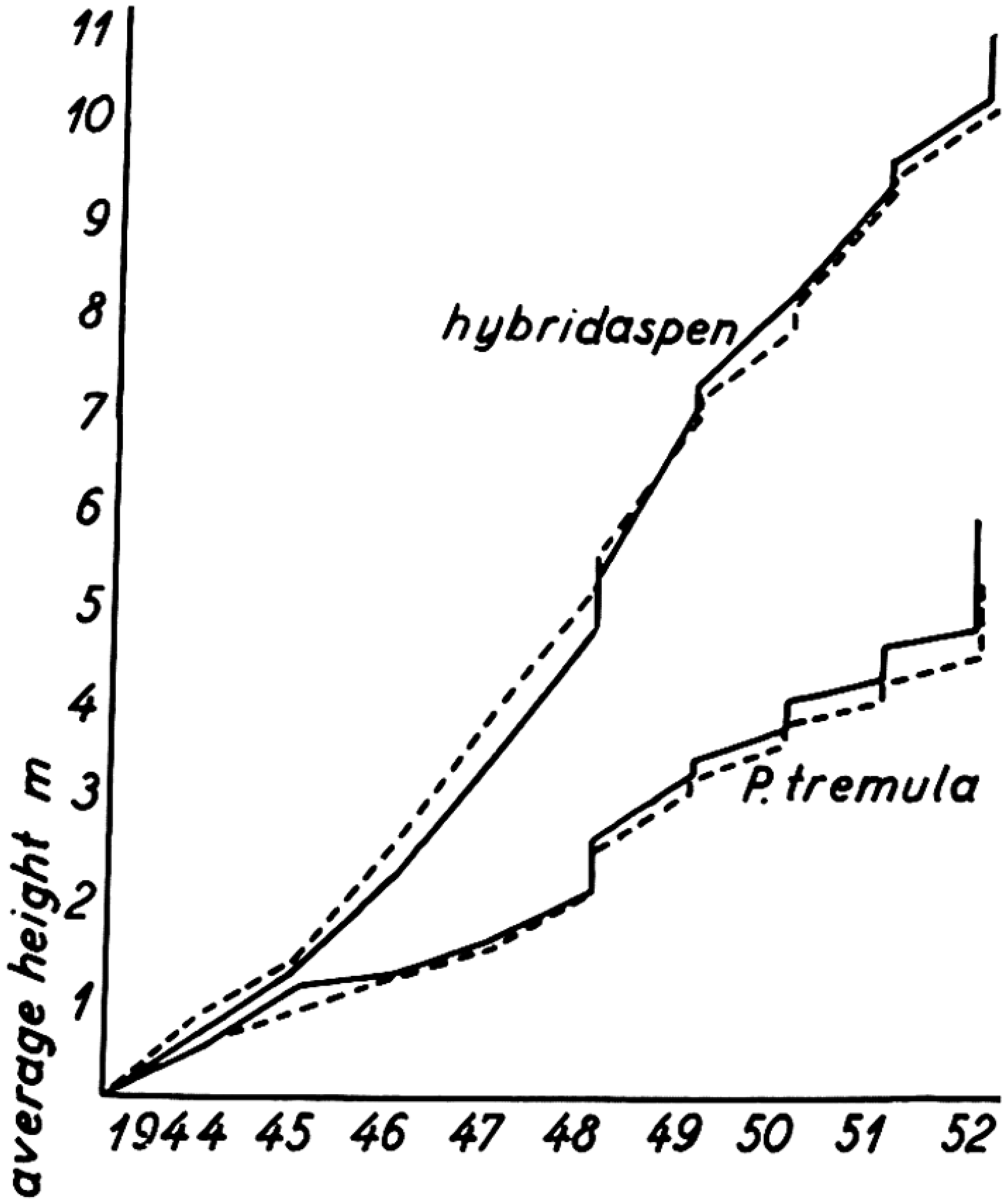


Fig. 55. Height-growth of hybrid aspen and *P. tremula* with 38 (diploid) and 57 (triploid) chromosomes in an 8-year-old experimental plantation at Ekebo, Sweden. Solid lines show families with 57 chromosomes (triploid), dotted lines families with 38 chromosomes (diploid). From Helge Johnsson, (l.c. 1953).

diploid chromosome number. Lastly, as shown in the foregoing, very promising triploid species hybrids have been discovered.

A direct comparison between diploid and triploid species crossings occurs in forest trees only in some material, which has been reported from the Swedish side and from which Fig. 55 is borrowed (H. JOHNSSON: "Hybridaspens ungdomsutveckling och et försök till framtidsprognos," *Svenska Skogsvårdsföreningens Tidskrift*, 1953).

The curves in Fig. 55 show the height-growth for four eight-year-old off-spring of *Populus tremula* and of the hybrid between *P. tremula* and *P. tremuloides* for diploid and triploid plants respectively. The families in the experiment are further related by pairs in that the diploid family always has the same mother as the corresponding triploid. The dotted lines represent the diploid plants (thirty-eight chromosomes), whereas the solidly drawn lines refer to the height of the triploid families. A distinct impression is obtained of a very considerable superiority in favour of the species crossing. It is far greater than any question of whether the plants are diploid or triploid, although the latter are the larger in both cases.

Although this is an excellent piece of work, yet it must be pointed out (as the author in fact does) that there still is only this one basis for comparison. The immediate impression, however, is in favour of the view that results are quicker through heterosis on the basis of species crossing.

Just as we search "upwards" for increased chromosome numbers in order thereby to obtain increased opportunity for combinations, there is also the possibility of searching "downwards" in the same way for decreased chromosome numbers in order thereby to secure the contrary advantage of fewer opportunities for combinations. If only we could call upon haploid plants for the work of breeding, considerable advantages might be reaped. The haploid chromosome number is the one occurring normally only in the sex-cells; but now and then plants arise which have the haploid chromosome number in the vegetative cells.

Haploid plants can appear by crossings between species rather distantly related, in such a way that the outside pollen does not enter into the fertilization, but merely stimulates the ovule to unsexed development of this nature. Moreover, in favourable circumstances they are produced from seeds with two embryos, so-called twins, which from time to time also occur in forest trees. The plants which have arisen from twins quite often have anomalous chromosome numbers. They may be polyploids, but may also be haploid. We must be very much on the look-out for such opportunities, although results are not so far known of their use in forest-tree breeding.

The slow succession of generations of forest trees is also a very good reason for trying this procedure. Should it prove to be successful it amounts to an opportunity of saving generations, and these are costly in forest-tree breeding. Haploid plants are almost always sterile, which has very naturally led to small interest being taken in their possibilities in plant-breeding. It has been shown, however, that after doubling their chromosome number they acquire fertility, and in that way plants of great value for utilization of heterosis have arisen. It acts like inbreeding of generations in order to achieve homozygosis, which is a pre-requisite for the employment of heterosis within the species. (SHERRET S. CHASE: "Monoploids in Maize," pp. 389–399 in JOHN W. GOWEN: *Heterosis*, Iowa State College Press, 1952.)

When WOODWORTH in 1929 had found the first tetraploid plants of alder, he was successful in demonstrating the first known instance of apomixis in a forest tree. He found it in *Alnus rugosa*, where it was controlled by isolating the female flowers in paper bags (R. H. WOODWORTH: "Cytological Studies in the Betulaceae. III. Parthenogenesis and Polyembryony in *Alnus rugosa*," *Bot. Gaz.*, Vol. 89, 1930, pp. 402–409).

By *apomixis* is meant the peculiar phenomenon that plants set viable seeds without previous fertilization. It is a "virgin birth", if you like. Apomixis occurs *inter alia* as exceptions in species which are otherwise perpetuated by normal sexual reproduction, and it is these exceptions that are of interest in this connection. It may take place entirely without pollen being present, and it may take place by the action of outside pollen in such a manner that the pollen involved does not participate in the fertilization. It acts merely as a stimulus, which causes one of the female vegetative (diploid) cells of the individual to be prompted into the development of a seed; it behaves as a heritable character, whereby the plant can achieve propagation through seeds, without doing so by a fertilization; it has greater resemblance to vegetative dispersal as a clone. Where haploid plants arise as the result of a similar "abortive" attempt at fertilization, the haploid chromosome number contained in the ovule is retained in the vegetative tissue of plants produced from it. With apomixis, the same chromosome number in the vegetative tissue is preserved in the succeeding generations, as is found in the plant from which they are derived. With the same chromosomes are also preserved the same inherent tendencies from generation to generation, and apomixis can therefore offer considerable advantages in forest-tree breeding. In this country it has been the subject of experiment in the case of plants which have arisen spontaneously.

In a rather large lot of plants of *Alnus incana*, which was planted in our Arboretum, a small early-flowering plant was found which was later identified as *Alnus rugosa*. Not only did it flower abundantly when a few years old, but it was peculiar in that almost without exception the flowers were female. Male flowers were insignificant or quite absent. After controlled pollination with *Alnus cordata* the seed germinated well, but there were no hybrids. All plants developed in the very image of the mother, so that it was reminiscent of clone formation. Later the plants of this progeny were further examined, and this made it certain that here was a case of apomixis. It did not even need to have outside pollen to help. Plants have given viable seed like this after the most efficient isolation in a greenhouse, where their flowering had ended before any flowering of the other *Alnus* grown in the Arboretum.

A similar instance of apomixis was discovered occurring spontaneously in alder in one of our forest districts (Buderupholm). This example was particularly interesting in that it was the forestry qualities of the " type " which first attracted attention. It was characterized by good growth in youth and a heavy foliage, which made it well-suited as a nurse tree. Its peculiarity of not attaining a great age gave it in a remarkable manner very great value in this connection, as it languished and died about the time when it had done its work and the costs of cutting it out were saved. It was found by hundreds of thousands as plants in the district nursery, and much seed of it was despatched to other districts, before any idea of apomixis was suggested. It has since been carefully tested and cytologically examined by C. A. JØRGENSEN, who is preparing a publication. It may be mentioned in advance, however, that a type of forest tree of interest in forestry has been discovered, which can be utilized through the medium of apomixis.

Although it is a matter rather far removed from forestry, reference should also be made to some investigations into grasses of the genus *Poa*, where apomixis is common. Many studies have been carried out, amongst other places at Stanford (California), by the Division of Plant Biology of the Carnegie Institution of Washington. From the annual report (Carnegie Institution of Washington: *Yearbook* No. 48, for the year 1948–1949, pp. 97–103), attention is merely drawn to some remarks in connection with breeding, which are referred to along with a general account of apomictic hybrids which have been raised. It says, amongst other things, that " The apomictic non-segregating *Poa* progenies are on the whole much more vigorous than the sexual, segregating ones ". On a single very promising one it goes on: " A very vigorous, fertile, and adaptable apomict has arisen . . . from a weak apomictic hybrid of *Poa ampla* × *pratensis alpigena*. The particular F_1 parent of this new apomict is itself apomictic, but it was a non-flowering dwarf at Stanford, though fairly vigorous at Mather and Timberline, where it ripens seed. Most of its offspring are uniformly weak and vegetative at Stanford like itself, but a few of its aberrants are vigorous and flower freely. One of these is the new apomict, which is both very fertile and highly apomictic. It is vigorous like *ampla*, rhizomatous like *alpigena*, rust-resistant, and apparently better adapted for contrasting climates than either parent of the original hybrid." All this perhaps may sound rather involved to a forester's ear, but these and other phenomena " must be considered in breeding work ". It would be wise to show a keener interest in apomixis in forest-tree breeding.

As early as 1889, ALICE H. RICH (*Bull. Torrey Bot. Club*, Vol. 16, 1889, p. 112) mentioned a tendency of *Alnus serrulata* Willd. (*A. rugosa*, Spreng.) to occur as purely female individuals. This reminds us of the appearance of the apomicts later discovered in this country. We must fasten our attention upon such plants and at the same time be on the watch for apomixis when working with hybrids.

To conclude, we must revert to the general statement about the inheritance of inherent tendencies (genes). It has been said that the genes are located in the chromosomes, and that the number of chromosomes is normally constant within the species. If we ignore the idea of mutations, the obvious thing is to regard self-pollination as the shortest way of arriving at identically twinned tendencies (homozygosis).

Inbreeding means crossing between closely related individuals, and the most pronounced form of it is self-pollination. It leads to homozygosis more speedily than any other form of breeding and thus to constancy in the inherent tendencies. In the course of a few generations it is possible by this procedure to arrive at the desired uniform material, for in the generations which are bred only those genes occur which existed in the limited chosen initial material. This method of procedure has also been used more than any other in breeding work, in the breeding both of livestock and of crop-plants.

It is therefore of the greatest importance to have investigated the extent to which it is possible to employ inbreeding in the improvement of plants in forestry. It would be most advantageous if we could make use of self-pollination, for through it we could have in as short a time as one generation a possibly embarrassing gene brought to some extent under control.

If we assume that an undesirable attribute such as, for example, curving or twisting of the stem, is determined by a gene A, and call the corresponding recessive gene a, then a tree with the combination AA would not be able to give any result by self-pollination, whereas, on the other hand, a tree which is heterozygotic in respect of this tendency and thus contains the combination Aa, will furnish progeny containing plants in the proportion of 1AA:2Aa and 1aa. We have thus obtained half of the plants homozygotic with reference to this attribute, and half of these plants are again homozygotic from containing aa and have been freed from curving or twisting of the stem, which will likewise be excluded from the progeny of these plants, unless it is brought in from outside.

A pre-requisite would be, that the species are monœcious, having female and male flowers on the same tree, and that is the case in by far the overwhelming number of economically important forest trees. In the next place, we must not leave this matter without a reference to the fact that experience has been obtained, from agricultural plants, that plants normally pollinated by outside pollen undergo self-pollination with difficulty. Compared with forest trees many such plants are already to a considerable extent products of cultivation (homozygotes). It must further be remembered that a possible and very probable inbreeding depression may be eliminated by crossing with other individuals inbred in the same way, so that they may be very valuable, although in themselves they are less vigorous.

Only experience can furnish information on the possibility of using self-pollination in the case of forest trees. However, we already have self-pollinated plants of *Fraxinus excelsior*, species of *Larix*, *Picea Abies*, *Pinus sylvestris*, *Thuja plicata*, etc., and the position really looks promising. All that is needed is far more work. In this connection it must be remembered that the various individuals of the species may behave differently, and that the fertility does not need to be high for the progeny to be valuable. Among the latest works, reference may be made to A. L. ORR-EWING: " Inbreeding Experiments with the Douglas Fir " (*Forestry Chronicle*, 1954). Cf. GEORGE I. ALLEN: " Parthenocarpy, Parthenogenesis and Self-sterility of Douglas Fir " (*Journal of Forestry*, 1942). See also p. 24 regarding KOLESSNIKOFF.

In the chapter on " hybrids " we have seen examples of results of species crossings. This is the use of heterosis on the basis of crosses between two species " unrelated " to one another. It is possible that inbreeding (perhaps even self-pollinations) in the species may become a decisive step forward in improvement within the individual species in the case of our forest trees. By raising types, which are each inherently homozygotic, types can be obtained which differ very much from each other. Each by itself may contain valuable tendencies which differ one from the other, and be deficient only in vigour of growth. By mutual crossing heterosis may result, so that a specially vigorous progeny is obtained, which at the same time has combined only the valuable tendencies present in the two types (JOHN W. GOWEN: *Heterosis*, Iowa State College Press, 1952).

In forest-tree breeding we have to overcome difficulties of cross-fertilization, which primarily is a matter of the difficulties of recognizing and fixing the good genotype. Of these we can easily solve the latter, of fixing the genotype, if we make use of the vegetative propagation of forest trees, and the problem of the better or poorer genotype has also become eclipsed by the outcome of heterosis. MOGENS WESTERGAARD puts it in this way: " It can scarcely be doubted that the heterosis method is the answer to breeding difficulties due to cross-fertilization. In fact it eliminates entirely the two unsolved problems, determination and fixation of the good genotype " (*Arvelighedslaeren*, 1953, p. 291).

It is one of the most important tasks of forest-tree breeding to work along these lines. We must admit that we lack much knowledge of the reaction of our forest trees in respect of in-breeding, but on the other hand vegetative propagation and the long life of the individuals give us very special opportunities to apply the results of inbreeding technically. This is one of the most promising and absorbing aspects of forest-tree breeding.

CHAPTER XI

BREEDING OF LARCH

AFTER going over the various links in the breeding of forest trees, an attempt will be made to summarize the work in an example. For this the choice falls on larch, which has long been subjected to experiment and provides the opportunity to deal with most aspects of the work.

Like the majority of the economically important forest trees, the larch has the flowers of the individual sexes clustered in a special inflorescence, and there are inflorescences of both sexes on the same tree (monœcious). In this, contact is made with the problems of flowering, which are most commonly to be found in the case of forest trees. The larch has the advantage of flowering at a relatively early age: although, as with most other forest trees, flowering does not take place regularly every year, yet it is nevertheless relatively uniform and abundant.

It is usually regarded as having a valuable timber. Seen from a breeding viewpoint one is tempted to do something just because of the great difference in value of the good products in comparison with the poorer ones. The timber should be sound, with no wounds or knots, and it should be grown to large dimensions of regular growth, in order to command a high price. The smaller and less well-shaped trees most often fall below those of other species in value. As this tree-species in artificially managed forestry has certain biological qualities, by being, for example, a deciduous light-demander with a favourable effect on other tree-species, foresters would like to work with it on many sites. In order to be justified economically, it should be used only in the form of types with really well-shaped trees, immune to disease.

The larch species are characterized by being found at the farthest outposts towards the north in Canada and Siberia. There is larch at the forest limits in the European Alps; the Japanese larch is amongst the last forest remnants on Fujiyama, while larches are among the most prominent mountain trees at other places in Asia; and in the Rocky Mountains we have larch, which form cover for the last remnants of *Abies* and *Picea*. While larch can contribute in that way to " raising the forest limit ", we also find economically important stands of it in such different localities as the Scottish mountains, New Zealand, and Denmark's lowlands.

Larches are divided into a number of species with a considerable difference in the extent of their geographical range. Within the species, moreover, various types (ecotypes) have been established as occurring in different geographical regions; this has been most clearly shown for the European larch, for which it was first pointed out by CIESLAR (*Zentralblatt für das gesamte Forstwesen*, 1899, 1904, 1907, 1914). This has later been the subject of intensive studies including a broadly planned experiment, amongst others, which was initiated by the International Union of Forest Research Organizations in 1944. There is, moreover, in larch a considerable individual variation, and both in nature and under cultivation species hybrids have been found to occur.

Furthermore, larch attracted early interest in afforestation far beyond its natural ranges. It was quickly used over a great part of Germany, and about two hundred years ago we introduced it from there into Danish silviculture. However, the importation of the European larch into Scotland is best documented and most generally known. It is thought to have first been brought there by the Duke of Atholl in 1738. Some few plants were planted, from which it gained wider popularity as a " Scottish larch ". On the basis of home-bred seeds a total of two hundred and seventy thousand plants was produced in Scotland from 1774 to 1783. In Denmark we have preserved a stand of European larch, the seed for which must have come from eastern North America round about 1800, so that as early as that time it had got so far as to cross and re-cross the Atlantic Ocean. It came to Norway and Sweden from Scotland about the year 1800. All this is evidence of its early spread in cultivation.

The cultivation of larch has also been marked, however, by much uncertainty, which has mainly been due to its being attacked by a disease, the larch canker, *Dasyscypha Willkommii*, Hartig. It is primarily the ravages of this disease which have been the limiting factor for its spread in cultivation, although the yield is also determined by the need to adopt a suitable method of planting. It is rather a tree for mixtures, and should not be used in too large uniform blocks. It was a matter of decisive importance that, after the spontaneous occurrence in Scotland of hybrids between Japanese and European larches, a definite resistance to the larch canker was observed. The hybrids were not only highly resistant, but they were also of vigorous growth and had a form most reminiscent of European larch, which gave additional hope for an extended cultivation of larch. (See above under " hybrids ".)

Through the first importation of European larch to Scotland, by using some few plants from a geographically restricted locality and by widespread seed-production from these trees and from their progeny, a start was made in the production of a type under cultivation. It is mentioned in forestry literature as " the Scottish larch ", and is praised for its beautiful form. Later, unfortunately, it ceased to reign supreme, because a good deal of other seed reached Scotland. In 1798 a small lot of larch plants reached Oldenburg in

Germany from England or Scotland and it was, perhaps, a sample of the "Scottish larch". It was subjected by one man, KRÖMMELBEIN, to careful selection through six generations in the course of his seventy-one-year forestry practice. Although he worked there only with free, uncontrolled pollination, this is, nevertheless, an example of a type produced under cultivation. (*Zeitschrift für Forst- und Jagdwesen*, 1888.)

In order to test and make use of the opportunity offered by hybrids, research was taken up into artificial pollination and vegetative propagation. LEVEN undertook the first controlled crossings between Japanese and European larches in Scotland in 1924–1925 (*Quarterly Journal of Forestry*, 1949). In Denmark our first successful controlled pollinations date from the spring of 1930, and grafting of larch has been done since 1932. All this was inspired by the hybrid larch that had spontaneously appeared in Scotland, of which MURRAY in 1915 had described a stand on Murthly Estate, where it had been planted in 1908 as three-year-old plants. (J. M. MURRAY: *Transactions of the Royal Scottish Arboricultural Society*, 1915.)

Before that time in several countries much work was done with provenance trials, which demonstrated the considerable variation of the European larch according to different geographical origin and provided evidence of great variety of form in the case of Japanese larch.

In botanical gardens and arboreta there had been collected a considerable representation, too, of the rarer species and varieties. Use had also long been made of grafting in order to preserve peculiar forms for horticulture, and OPPERMANN had suggested the possibility of increasing thereby the number of valuable seed-trees. Finally, there was a copious botanical literature available, so that abundant resources were at hand for taking up deliberate breeding-work on the basis of controlled pollinations and vegetative propagation.

It only has to be systematized and turned to account in breeding. It is not enough to graft in order to get several seed-trees; it is most important to be at the same time sure of the correct pollination. It is therefore necessary to carry out more intensive investigations of the flowering conditions, to use "tree-shows", "seed-gardens", and much more. The great work which was carried out before 1930 must on no account be undervalued, since it forms the basis for the breeding work undertaken at that time. The stage had then been reached of using only vegetative propagation in horticulture and in botanical collections, and the use of seed on the basis of free, uncontrolled pollination had not been superseded.

After about twenty-five years of breeding work we are now getting near to the practical application of the results of improvement. It should be observed that the work with other tree-species to be done in the future or now proceeding should not take so long a time in achieving similar results.

It must be remembered that the work on larch-breeding has been carried out with a simultaneous general evolution of technical aids and establishment of institutions.

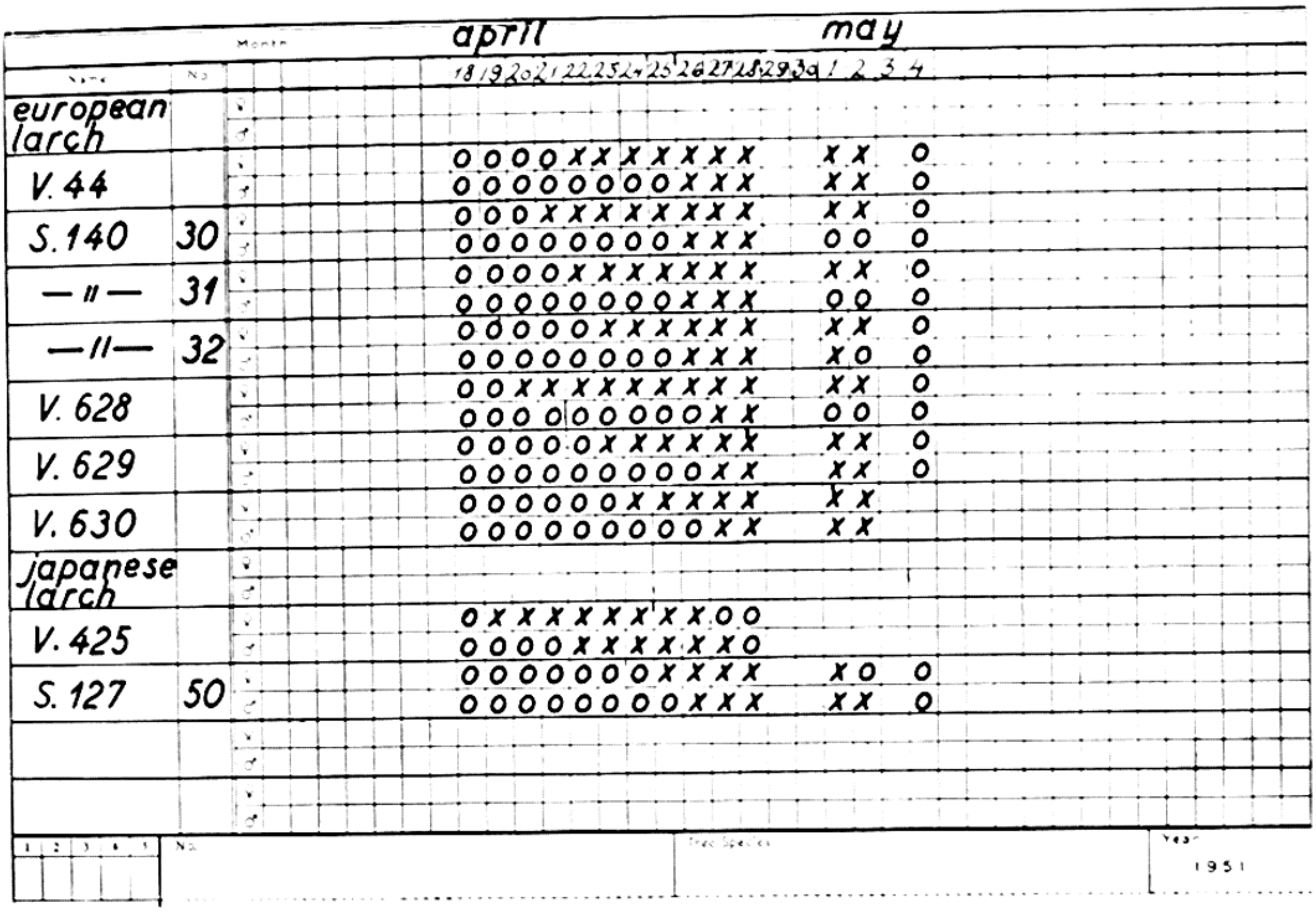
The technique of controlled pollination prevails universally and without heavy expense; in that way sufficient numbers of progeny have been created for forestry trials. A step forward of several generations has been made. Vegetative propagation is very reliable and has become cheap and "tree-shows" and "seed-gardens" have been established. Species hybrids are under control and being used more and more. The most dangerous enemy of the larch, *Dasyscypha Willkommii*, we need fear no longer. The larch does not have to occur only as a diploid; it is now known both as a triploid and as a tetraploid. Larch has proved to be well adapted for self-pollination, and there are signs that further results can be attained through inbreeding and use of heterosis. Altogether it shows progress which might not have been anticipated in all its aspects, and it gives grounds for further optimism.

The *controlled pollination* is carried out according to the same plan as in the early years, see Figs. 7 and 8. There has been some interchange between parchment and bags of "Cellophane" and other similar more transparent materials. The use of simple parchment bags is cheap and speedy; they are to be recommended, although now and then some of them are lost by injuries.

Flowering takes place before or just at the commencement of leaf-flushing. The pollen is easy to collect and to store, whereas it may be rather difficult to distinguish female and male flowering buds from each other sufficiently early. This may mean that the work has to be done quickly over a few days, in order to be able to have the males removed with certainty and only the female flowers left isolated. This need not prevent a considerable number of isolations being effected. If the flowers are placed conveniently and in abundance, as in the clone shown in Figs. 2 and 3, an expert assistant will be able to do about twenty-five isolations per hour. This includes removal of the males and fixing of double bags.

In a good flowering year it is not difficult to find five or six female inflorescences in each isolation. If we assume that on the average they furnish five cones, and that each of these will supply only ten viable seeds, with five hundred isolations it should be possible to get about twenty-five thousand useful seeds, which is a conservative estimate. One must not allow oneself to be led to believe, however, that all has gone well, merely because the cones develop normally. There is pronounced false fruit-setting or parthenocarpy, and cones will be obtained with seemingly well-developed seed even when there has been no fertilization.

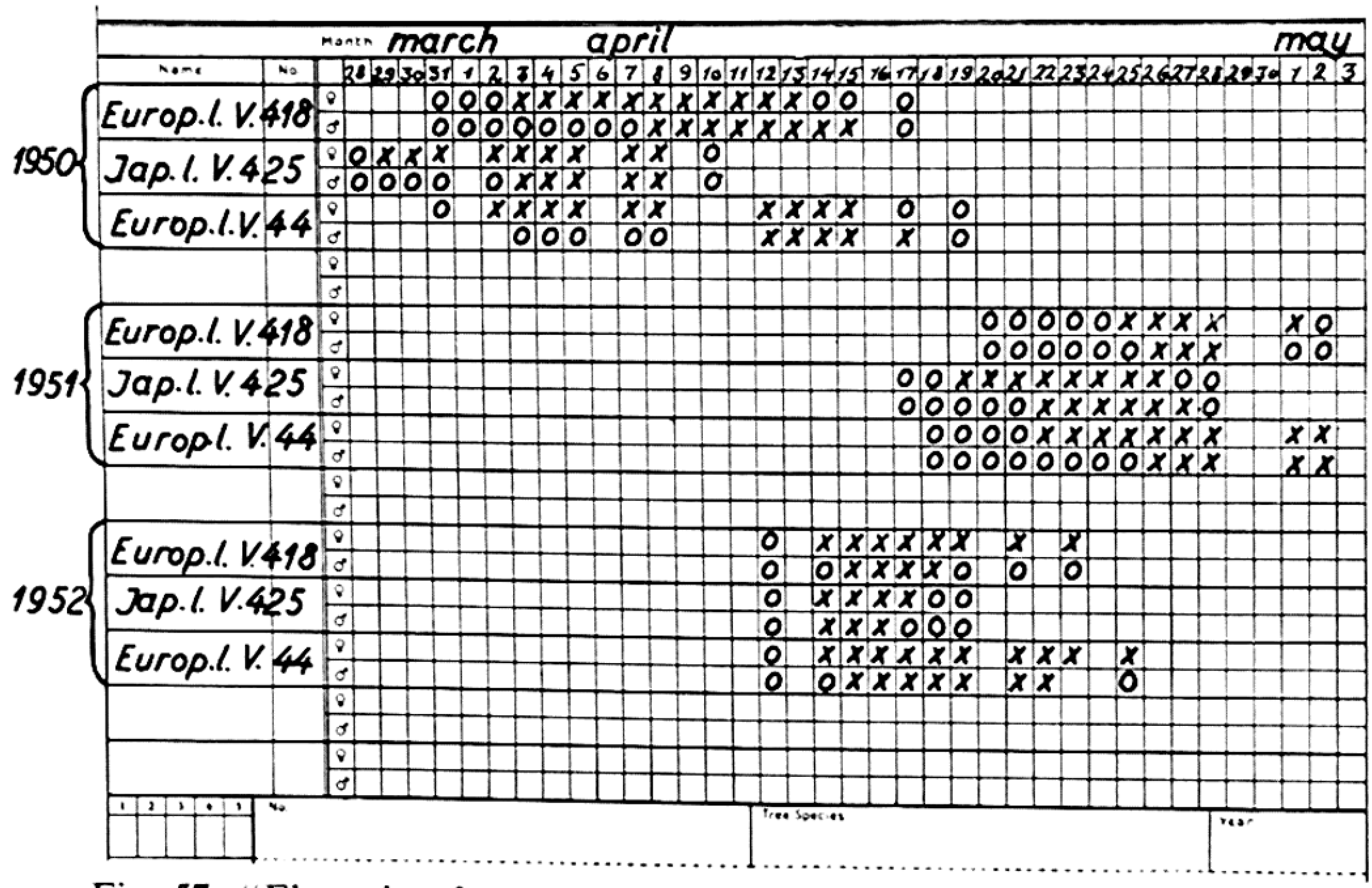
With larch, just as with many other conifers, there is a difference in the time of the expansion of the female and male inflorescences on one and the



		Month	april													may			
Name	No.		18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4
european larch		♀																	
		♂																	
V. 44		♀	o	o	o	o	x	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	x	x	x			x	x		o
S. 140	30	♀	o	o	o	x	x	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	x	x	x			o	o		o
— " —	31	♀	o	o	o	o	x	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	x	x	x			o	o		o
— " —	32	♀	o	o	o	o	o	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	x	x	x			x	o		o
V. 628		♀	o	o	x	x	x	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	o	x	x			o	o		o
V. 629		♀	o	o	o	o	o	x	x	x	x	x	x			x	x		o
		♂	o	o	o	o	o	o	o	o	o	x	x			x	x		o
V. 630		♀	o	o	o	o	o	o	x	x	x	x	x			x	x		
		♂	o	o	o	o	o	o	o	o	o	x	x			x	x		
japanese larch		♀																	
		♂																	
V. 425		♀	o	x	x	x	x	x	x	x	x	o	o						
		♂	o	o	o	o	x	x	x	x	x	x	o						
S. 127	50	♀	o	o	o	o	o	o	o	x	x	x	x			x	o		o
		♂	o	o	o	o	o	o	o	o	x	x	x			x	x		o
		♀																	
		♂																	
		♀																	
		♂																	

1 2 3 4 5 | No. | Tree Species | Year 1951

Fig. 56. "Flowering form." Designed by H. Barner. In general use in Denmark. *x* stands for an accessible or pollinating flower, *o* for a closed or non-pollinating flower. The forms are printed and the date and any additional information desired are filled in. In the example shown some records for a number of trees of larch have been entered. It indicates, amongst other things, the commonly occurring metandry, *see* Fig. 12.



			Month	march				april																														may		
	Name	No.		28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3
1950	Europ. l. V. 418		♀				o	o	o	x	x	x	x	x	x	x	x	x	x	x	o	o		o																
			♂				o	o	o	o	o	o	o	o	x	x	x	x	x	x	x	x		o																
	Jap. l. V. 425		♀	o	x	x	x		x	x	x	x		x	x		o																					
			♂	o	o	o	o		o	x	x	x		x	x		o																					
	Europ. l. V. 44		♀				o		x	x	x	x		x	x				x	x	x	x		o		o														
			♂							o	o	o		o	o				x	x	x	x		x		o														
			♀																																			
			♂																																			
1951	Europ. l. V. 418		♀																								o	o	o	o	o	x	x	x	x			x	o	
			♂																								o	o	o	o	o	o	x	x	x			o	o	
	Jap. l. V. 425		♀																					o	o	x	x	x	x	x	x	x	x	o	o					
			♂																					o	o	o	o	o	x	x	x	x	x	x	o					
	Europ. l. V. 44		♀																						o	o	o	o	x	x	x	x	x	x	x			x	x	
			♂																						o	o	o	o	o	o	o	o	x	x	x			x	x	
			♀																																			
			♂																																			
1952	Europ. l. V. 418		♀																o		x	x	x	x	x	x		x		x										
			♂																o		o	x	x	x	x	o		o		o										
	Jap. l. V. 425		♀																o		x	x	x	x	o	o														
			♂																o		x	x	x	o	o	o														
	Europ. l. V. 44		♀																o		x	x	x	x	x	x		x	x	x		x								
			♂																o		o	x	x	x	x	x		x	x			o								
			♀																																			
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1 2 3 4 5 | No. | Tree Species | Year

Fig. 57. "Flowering form" used for combining observations over three years of two clones of European larch and one clone of Japanese larch.

same tree. It is seldom so pronounced that one cannot find open females and pollinating males at the same time. Even stronger or weaker sunlight on different parts of the tree can affect it. On the other hand, it is often so well marked that it can facilitate distinguishing between female and male during the isolation, and it is of great importance later on when the individuals are used in seed-gardens.

It is important to pay attention to this in the selection and subsequent appraisement of trees used in research and in breeding. The greater or less priority of maturing of the female flowers of individuals, their protogyny or metandry, is determined genetically and thus perpetuated in the clone. As in the case of the time of flowering, it is affected by the external conditions. The result is not the same if the flowering takes place in a sudden warm and dry period, when the whole flowering goes on quickly, compared with flowering which takes place in mild and moist weather. The latter prevents pollination but not the continued expansion of the female flowers.

Fig. 12 shows the larch with the female blossom open for pollination, while the male flowers have not yet been able to emit their pollen. Only a very short period with a situation like this in dry weather, otherwise favourable for the spread of other pollen, will ensure cross-pollination. Thus the only thing we have to do is to procure the correct pollination abundantly at the right time.

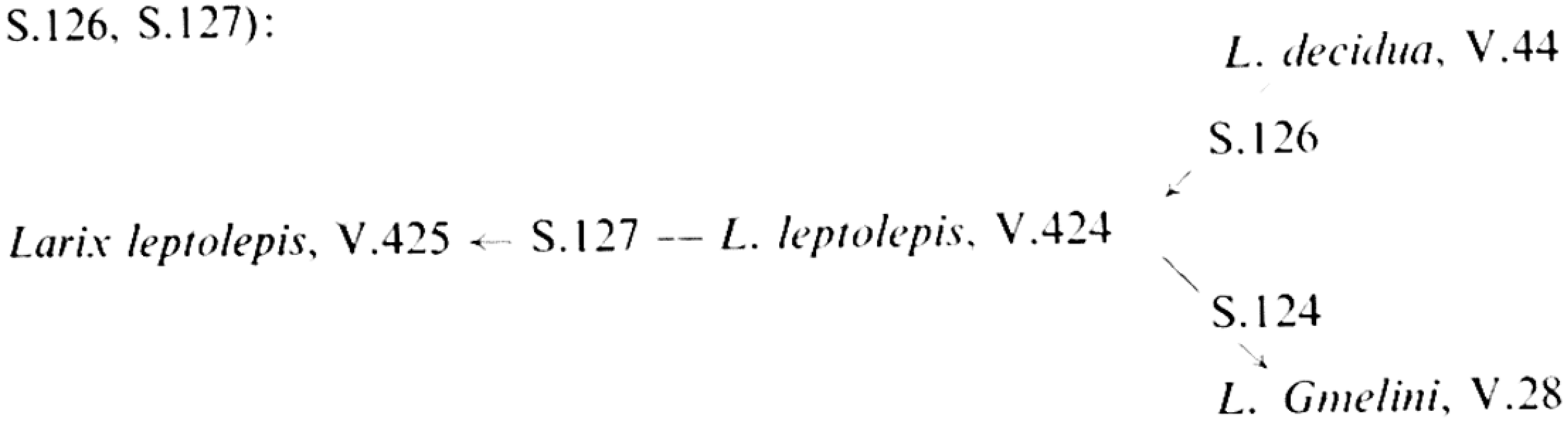
Once the clones of the selected larch have been brought together by grafting into " tree-shows ", or in some other way under so far as possible identical external conditions, year after year a comparative examination should be made of the flowering behaviour, until one has become familiar with the separate individuals. This can be done by making entries on a form like that shown in Fig. 56.

From observations over several years various comparisons can be made, as, for example, in Fig. 57, where three clones, one of Japanese and two of European larch, are summarized in respect of their flowering in three different years. In 1950 the flowering took place early and in 1951 late, but in both these years the Japanese larch was quite a number of days ahead of the European larch, in both female and male flowers. Moreover, in 1950 and 1951 there was pronounced metandry in the case of both the Japanese and European larches. In 1952 flowering fell between these two extreme points, but it occurred very suddenly, so that the difference in the advent of flowering was obliterated both between the individuals and between flowers of different sexes. The flowering took place that year in a markedly warm period, which suddenly followed the winter.

In order to illustrate developments in the use of controlled pollination with a limited amount of data, an example from the Arboretum at Hørsholm will be quoted. Pollination was carried out amongst the following four trees:

Larix leptolepis, V.424
.. .. V.425
.. *decidua* V. 44
.. *Gmelini* V. 28

They were combined in the following manner, and the progeny raised from them were distinguished by the bracketed sowing numbers (S.124, S.126, S.127):



These pollinations were made in the spring of 1933; sowings in 1934. At the same time two lots of *L. decidua* were included:

S.76: Sowing in the spring of 1932 as uncontrolled progeny from V.44, which has been picked out as the finest larch in Denmark (Fig 1).

S.140: Sowing in the spring of 1934 as uncontrolled progeny from a tree in a stand of 165 to 170 years of age, which is a remnant of one of the first plantations of European larch in this country.

We shall first form an opinion of how long a time must be counted upon to give a new generation.

In this connection it may be mentioned that some of the plants of S.76 had both female and male flowers in the spring of 1938 (at six years of age). In the spring of 1940 there was abundant flowering in the case of S.76 (at eight years of age), and little flowering in the case of S.127 (at six years of age). At that time preliminary controlled pollinations were carried out, but they were rejected later, as we had been reduced to using a small number of flowering individuals only, and there was thus no freedom of choice.

In the spring of 1941 and especially in the spring of 1942 (at eight years of age for the controlled pollinated plants) there was abundant flowering. There was plenty of choice of individuals as a basis for the next generation, and it was possible to obtain such an abundant progeny that they could become the basis of further experiment. Four trees of S.127 gave in all about five hundred isolations which, after being pollinated with one father S.140[1], provided 1091 cones, from which 3450 good 1/1 plants (S.556) were raised. It was most usual to get progeny amounting to one hundred to two hundred individuals from a single plant, but up to about one thousand plants were raised by controlled pollination from a single selected eight-year-old seedling. Because of the abundant production of pollen it was not difficult to arrange for progeny with a common father to be planned in respect of a large number of female flowers on a series of individuals. On account of the origin of the material it provided further opportunity to plan back-crossings, etc.

In controlled pollinations of larch with species like *L. decidua, leptolepis, Gmelini*, and hybrids of these we can thus claim to be able to get a sexual generation in about ten years. In this case we did the first controlled pollination with a large number in 1933; the second generation was established in 1941–1942; and the third generation was established in 1950–1951. We cannot, however, count on working so closely to definite years. We must certainly often halt on our way in order to arrange for a more intensive trial of a series of combinations through repetitions or the production of large lots of plants, before we are ready to proceed further. A warning should, in fact, be given against going ahead too quickly. Time should be given in order to get a general flowering over all the individuals of each generation, so as to prevent ourselves in any way from being tempted to make use of the individuals which flower earliest or most abundantly. Otherwise it is probable that we should find ourselves working with a material genetically endowed for early and abundant flowering. HELGE JOHNSSON has reported a case with *Betula* (H. JOHNSSON: "Hereditary Precocious Flowering in *Betula verrucosa* and *B. pubescens*," *Hereditas*, Vol. 35 : 1, pp. 112–114, 1949), and there are other examples of it.

It is not unreasonable to presume that now and then negative selection has been achieved by excessive eagerness to breed at home a new and rare species, whose expensive seeds may have been a temptation to economic exploitation. It is not impossible that this has had significance in the cultivation of *Hevea* in Malaya, and I am inclined to think that it has affected Japanese larch and Mountain pine in parts of this country.

Given time, therefore, in each generation, carry out a number of controlled pollinations on a wide scale, so that there is a certainty of making the best possible choice. In order to increase the number of plants raised by crossing between two selected individuals, they can be crossed both ways. Generally there is no reason for the assumption that these opposite crosses should give progeny which differ from a genetical viewpoint. It is quite another matter that one of the ways may be much easier from the technical point of view. This may be due to the favourable proportions of female and male flowers, or, for example, to one of the lots having larger cones, which more readily give up their seeds.

Vegetative reproduction of larch is most easily undertaken by grafting. The simplest procedure is grafting in the open on two-year-old stocks, which are firmly rooted after being planted out as one-year seedlings. The grafting is performed in the spring at the time of leaf-flushing with stored scions, which are cut off during the winter. A grafter with one assistant can graft about forty grafts an hour, and with appropriate methods of procedure there is only a small loss. In the first summer after grafting some pruning must be done and the young leader tied back. Transplanting is done in the follow-

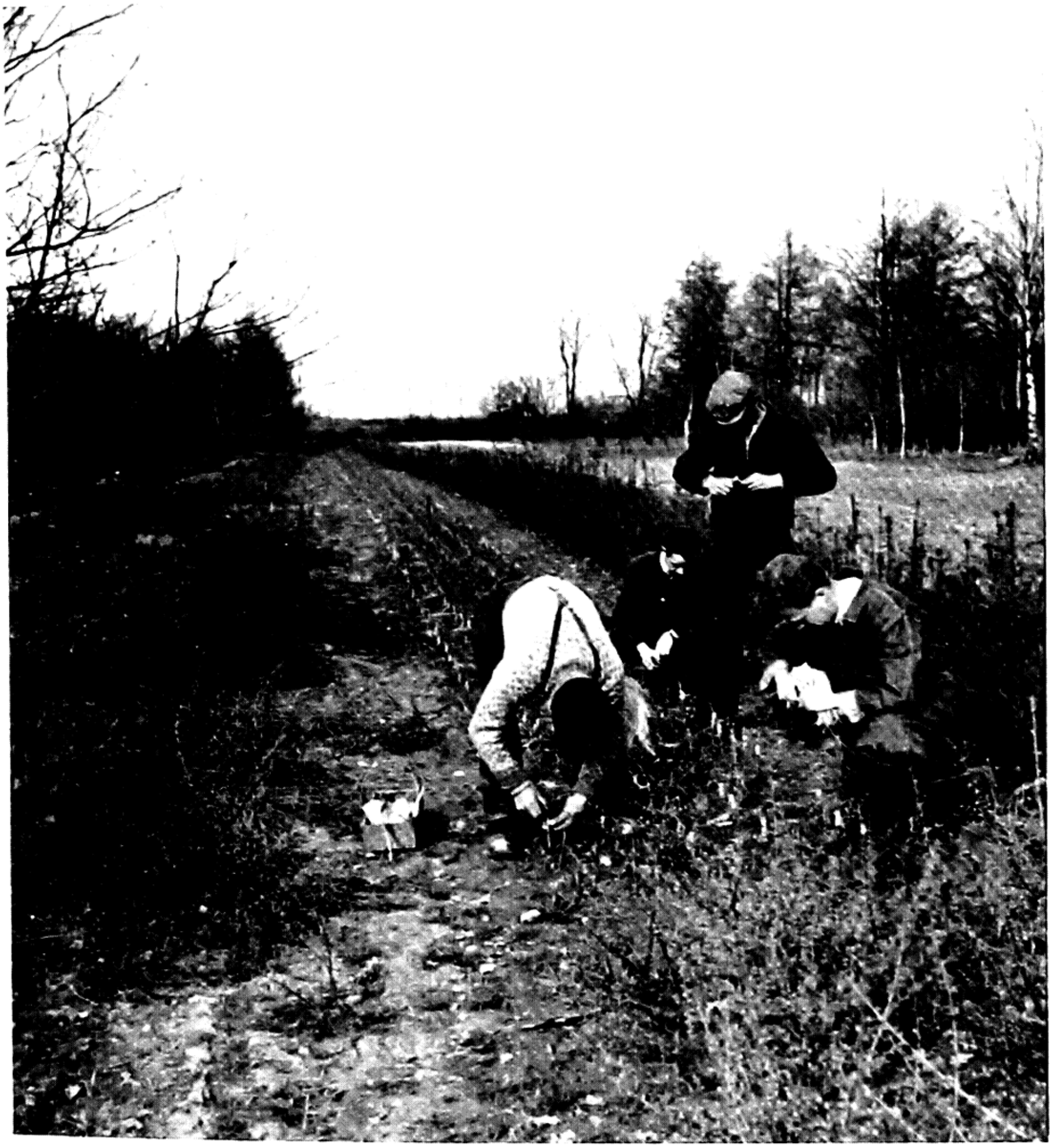


Fig. 58. Grafting of larch in the nursery. Photograph in the Arboretum, Hørsholm, 24th April 1950.

ing spring. The root has by then reached the same development as a 1/2 transplant, so that this is rather troublesome and must be done carefully. If it is desired to establish large collections of graftings, it can be an advantage to plant out the stocks as 1/1 and graft in the following year on the site where the plants are to remain. Grafting with well-ripened wood can be carried out in August–September, but is not much used.

If it is desired to use grafting in the greenhouse, the stocks must be potted as 1/0 in the spring and stood out in the open until the following winter. They must be kept so well protected that they can be taken up towards the spring and moved into the house, so that they stand in their pots as well-rooted 1/1 plants and are ready for grafting. Grafting in the greenhouse can go on very well, but care must be taken over the bottom-heat, which can kill the root. The scion can develop nicely without the root having begun to grow, so that promising plants may suddenly die off.

In the open and in the greenhouse side-grafting, whip-grafting, and bark-grafting are used with equally good results. The use of the various forms of grafting must in the first place be adapted to the thickness of the stock and the familiarity of the grafter with one or other of the grafting methods. No effects have been observed from the stocks having been of one species of larch or another. The rule for choosing stocks may best be expressed by saying that they should be vigorous and healthy plants. In spite of variation in the species used as stocks, an astonishing homogeneity has been obtained in the growth of the scions, and so far no stocks have been found which cause abnormally early seed-setting or dwarf growth.

Especially in the early years, before we were familiar with grafting larch, some very promising experiments had been initiated with cuttings. By using softwood cuttings in the summer, quite a lively root-formation can be obtained, but the difficulty lies in getting good shoot-formation and handling the transplantation, so that it has not come into general use. Nevertheless good plants can be raised in that way, and efforts to devise a satisfactory technique ought to be continued. Propagation by cuttings can present considerable advantages. It is, indeed, only the ease of grafting in the open which has temporarily diverted interest from cuttings.

In the open, grafting is not restricted to the use of small two-year stocks. In particular, where the object is the speediest possible multiplication of vegetative material, one can use with advantage a much older stock which can be five to ten years old or perhaps more, provided too broad and unworkable a cut surface is avoided. It must preferably be not more than about 5 cm. (2 ins.) in diameter, and some fresh needle-bearing branches must be retained on the remaining portion of the stem. As early as the first year after grafting, a manifold yield of scions can be taken from it, and in the second and third year it becomes even greater. In cases where it is possible to get only weakly or scarce grafting material, one can with great advantage interpose a "multiplication-garden", from which is obtained not only abundant, but also uniform, grafting material. (See also Figs. 14 and 15.)

Graftings of larch and seedlings produced from controlled pollinations have been used in the establishment of "seed-gardens". In one of the first established, the practice was adopted of combining the two in order to achieve production of hybrid seeds. It is so laid out that the seed is harvested from one clone of European larch, which is pollinated from Japanese larch. The latter were selected from a progeny produced after controlled pollination between two trees.

They were planted in rows at a spacing of 3 m. (10 ft.), so that rows of European larch and Japanese larch alternate. But the grafted plants of European larch and the seedlings of Japanese larch were planted at a spacing of 4 m. (13 ft.) in the rows. Pollinators, however, are not needed in that number. With regard to the clonal plants no thinning was prescribed until a number of years after the occurrence of the harvest and then only to give the individual trees more space. Use of the same number of seedlings in the case of the Japanese larch, on the other hand, gives a chance to make an early and heavy thinning, so that only the plants best adapted in respect of growth-form and time of flowering remain.

For the clone of European larch use was made of the European larch V.44 mentioned earlier, and the original tree is, at an age of about 180 years, perhaps the finest larch-tree in Denmark. Its progeny derived from free pollination has been known since 1932. It was used in controlled pollinations in 1930 and on several later occasions. Sixty-eight graftings in 1936–1937 gave in 1942 (at six or seven years of age) a yield of 3850 cones with $\frac{3}{4}$ kg. (1·65 lb.) of seeds, so that it has proved to be a good seed-producer. Moreover, the clone has been observed for several years during flowering, from which it has been proved to be distinctly metandrous (see form in Figs. 56 and 57).

The Japanese larch was the produce of two selected trees (V.424 and V.425), which from controlled pollination in 1933 gave the S.127 also mentioned above. From two selected plants (related in the first degree) in that progeny, S.127^{10} and S.127^{2}, was produced by controlled pollination in 1942 the progeny (S. 626) used in this case. All the pollinators employed are thus again related in the first degree, and from them a selection is made.

Planting of the seed-garden in question was carried out in 1946 with graftings and seedlings three years of age. The area is one hectare and it contains 242 clonal plants of European larch, whereas the original 240 seedlings of Japanese larch (S.626), nine years after the planting, have fallen to

190 in number. In 1948 (two years after planting) 1·5 kg. (3·3 lb.) of hybrid seed were harvested; in 1954, 13·7. kg. (30 lb.).

By using a single clone for one of the species, hastening of hybrid formation is achieved. When, as in this case, there is, in addition, well-marked metandry in the specimen used, its female flowers would normally have several days to be cross-pollinated before the first pollen from the clone's own male flowers made its appearance. By using as pollinators a selection of seedlings that have been to some extent inbred, it is true that related fathers are guaranteed, but they are not identical with each other and, amongst other things, they are somewhat variable in their time of flowering. There will thus be a high degree of assurance of thorough pollination even with a climate which varies from year to year. Moreover, there is the great advantage of having pollinators which are identical in the sense that they can all be regarded as being good, but still different from each other in tendencies. The progeny will therefore be satisfactory without being unnecessarily uniform, and that is a great advantage.

As experience has shown, however, that in the breeding both of pure species and of hybrids excellent progeny can be secured by crossing between single individuals, seed-gardens have also been established by other methods of procedure.

Some seed-gardens are composed only of clones which have been drawn as selected individuals from different stands, whereas others are composed of clones from the best trees of a single, fine stand. In order to obtain hybrid seed a series of seed-gardens has been established, each of which consists of only two clones.

As an example of another method of procedure may be mentioned the raising of hybrid seed between Japanese larch and European larch of the Scottish type. Of the latter, three individuals were selected in a local stand derived from seed obtained from Scotland. In the stand, which was as a whole excellent, they were " the most vigorous " (Scot 1), " the most finely branched " (Scot 2), and " the best all-round tree " (Scot 3).

After propagation into clones and control in a tree-show, mutual pollination was performed amongst the three clones, from which sufficient progeny was obtained of Scot 1 × Scot 2 and Scot 1 × Scot 3. Two seed-gardens were then established, in which one clone of Japanese larch was used. In one of these the Japanese clone was planted along with clones of Scots, 1, 2, and 3 respectively, whereas in the other area it was placed along with the progeny of Scot 1 × Scot 2 and of Scot 1 × Scot 3 raised by controlled pollination.

The advantage of the first seed-garden is that it gives control over the three clones of " Scottish larch " so that one or two of them can be removed, if that should seem desirable. In the second case there is the advantage that one may have new combinations of the genes contained in the three "Scots". There it becomes possible by constant thinning to concentrate those individuals that are esteemed to be best.

At the moment it is not possible to say that any one method is the best. Similarly, reliance upon one method of procedure or another must often be influenced by the material dealt with in each case. As a general rule it is recommended that the problem should be attacked simultaneously from different aspects so that, on account of an ill-founded belief in a certain "method", one should not involve oneself in a loss of time. In this as in other aspects of breeding time is more costly than increasing the work.

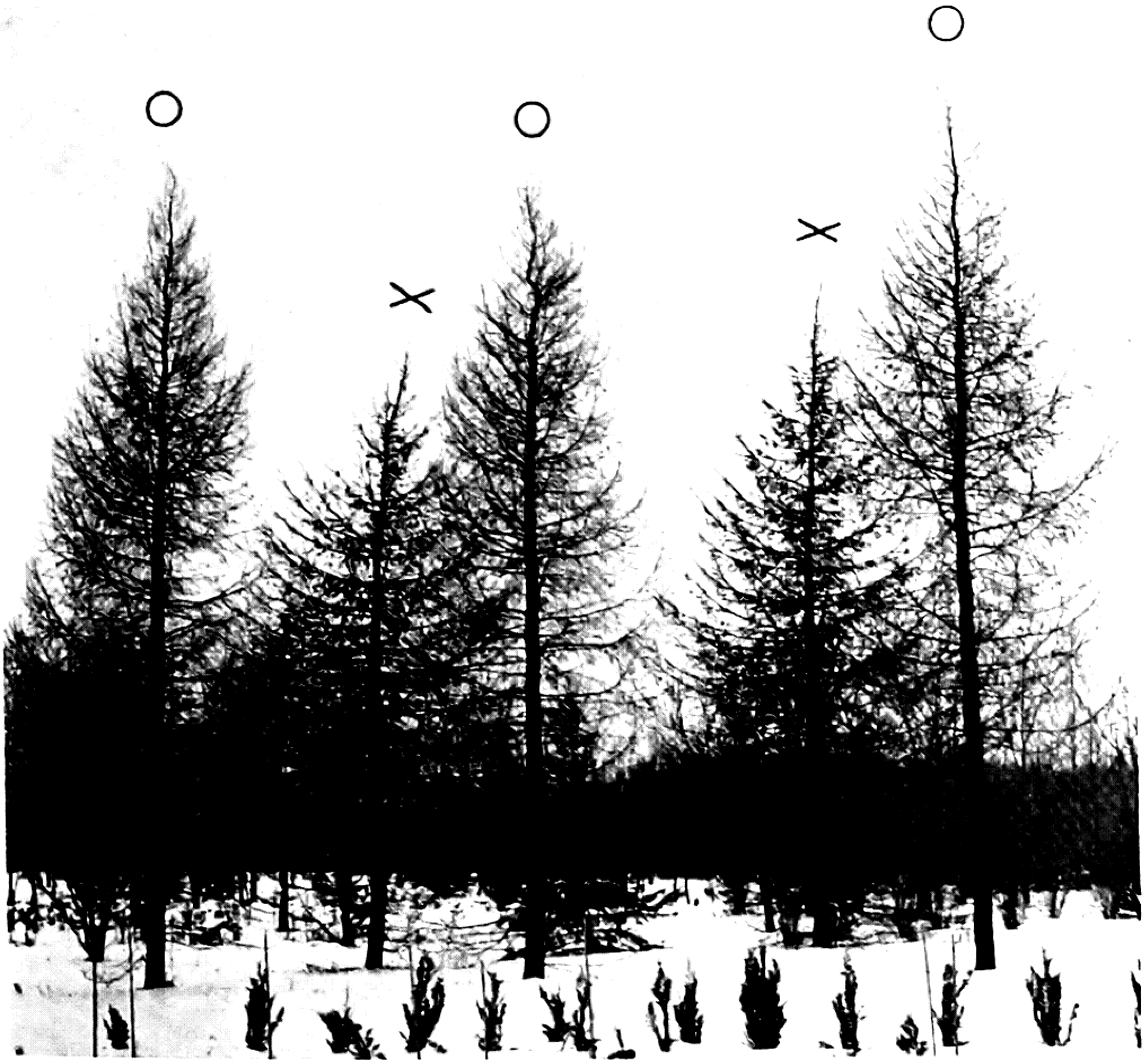


Fig. 59. A "tree-show" of larch, grafted in 1939. The three trees marked *o* were grafts from one tree (V.418). The two trees marked *x* were grafts from a second tree (V.413). Note the irregular formation of the top in the case of V.418 and the early cone-setting in the case of V.413. Photographed in the Arboretum, Hørsholm in 1954.

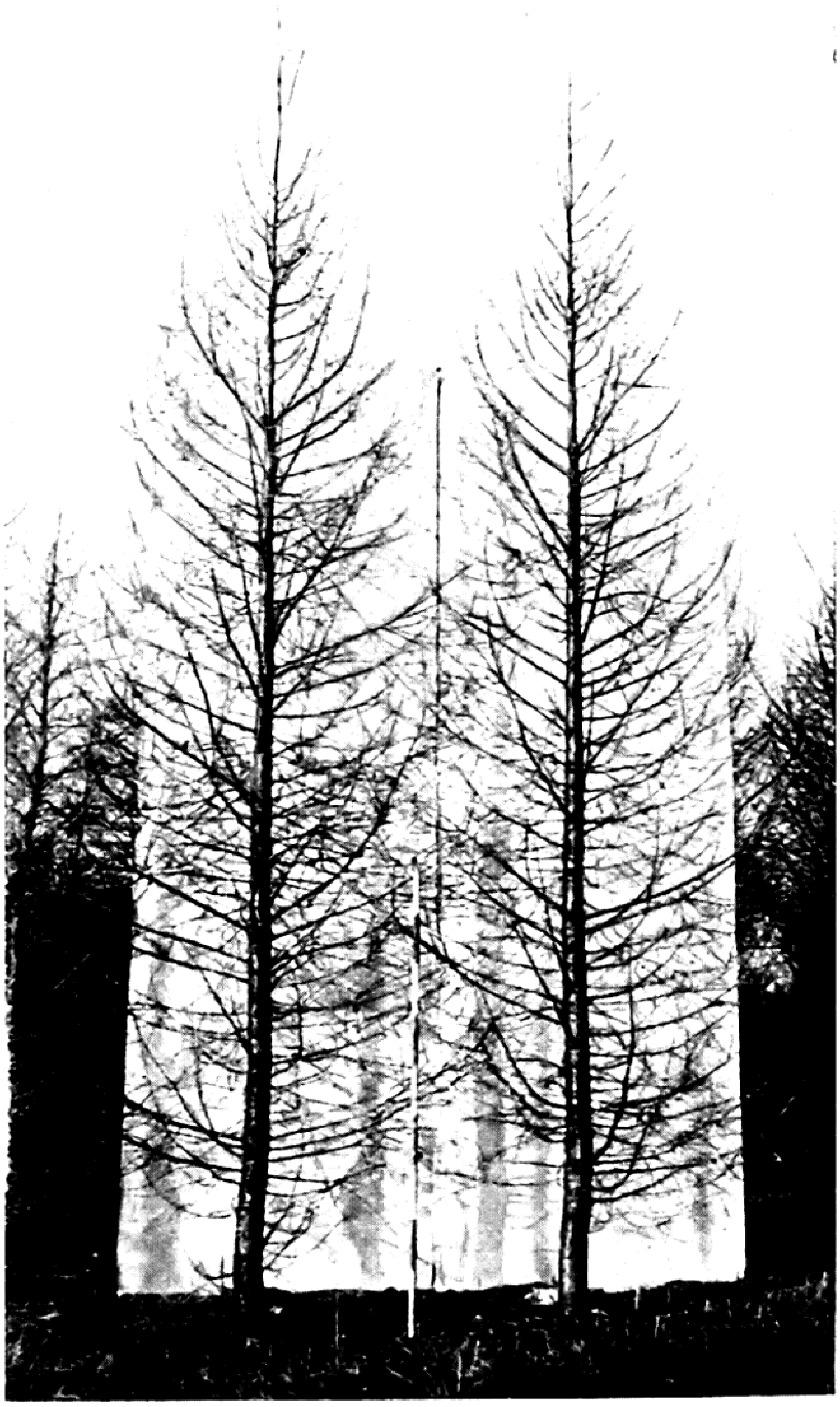


Fig. 60. Two grafts of one clone. Grown under the same environment they have grown up almost the living image of one another. In 1954 their heights were 10·8 and 11·2 m. and also in earlier years there has been a close agreement between the height and branching of the two trees. Grafted in 1939 from the tree shown in Fig. 47, which was the finest tree in the stand. When tested in a "tree-show" where the trees have grown uninfluenced by neighbours, they show a genotype of valuable form. The 13 years older tree in the stand was at the same time only 15·5 m. high, which may mean that under the given conditions it did not get a chance to show its full powers of growth. The fine tree which shows up badly in the stand, may under other conditions prove to be even more valuable. Photographed in the Arboretum at Hørsholm on 16th January 1947.

In a fifteen-year-old *tree-show* of larch, differences between the clones stand out very clearly. The trees at this stage have reached such a development that they also carry more conviction. Foresters have a tendency to want to have plants grown-on to a fairly " adult " size before they venture to place reliance upon an estimation of the inherent tendencies. That is wise so far as it goes, but it takes time. It is therefore worthy of remark that a close agreement has been found between the oldest tree-show, now fifteen years of age, and the observations which it was possible to make a few years after its establishment. This applies to flowering conditions, leader formation, and position and stoutness of branches. By using tree-shows it is therefore possible after only a few years to differentiate individuals with undesirable attributes, and that is a useful help.

We should not wait for faults to correct themselves with age. In one case a clone a few years after grafting turned out to have a distinctly crooked leader (V.418 in Fig. 59). It righted itself to such an extent that the same clone, now fifteen years of age, stands with a beautiful straight stem. That has only come about, however, by a filling-in of the curves, so that there is an additional defect due to the fact that the internal unsatisfactory structure is covered over. The clone in question was acquired for breeding on account of the good shape of the original tree with a slender symmetrical stem. The tree was of such a size and age, that the inclination was to regard a rather irregular formation of leader as having its origin in environmental effects. In the course of a few years only, graftings in a tree-show revealed the true position—that the curvatures of the leader were genetically determined.

As regards hybrids, no longer does any doubt prevail that they offer advantages. The problem is more how to place a value on these advantages. That can be done only on the basis of controlled pollinations, and after having them produced in such quantities that they can furnish evidence in respect of forest stands.

From one lot of hybrid larch, Japanese × European larch, such a large lot of plants was raised after pollination in 1935 and sowing of the seed in 1936 that it has been possible to make a trial of it in various ways. The plants were recorded in S.210 and their father was the European larch, V.44 (Fig. 1), mentioned earlier.

At the time of planting in the spring of 1939 of four hundred plants at 1·25 × 2·5 m. (4 × 8 ft.) apart of this lot of S.210, a similar plantation of European larch was put out beside them. The plants used for the latter were from a free pollination of V.44, which, in the form of the original specimen, stands surrounded in the forest by trees of its own age. The plants of the European larch were one year older than the plants of the hybrid. After two thinnings of the lots, fifteen years after planting a measurement gave the following result; in this the measurements for the two sample-plots, each of which contains about 0·15 ha. (0·37 ac.), have been converted to refer to 1 ha. (ac.):

	February 1948		February 1954	
	Hybrid S.210	European Larch S.180	Hybrid S.210	European Larch S.180
No. of stems	2540 (1016)	2710 (1084)	1106 (442)	1219 (488)
Diameter, cm. (Q.G.)	10·7 (3·4)	9·8 (3·0)	16·0 (5·9)	14·7 (4·7)
Height, m. (ft.) .	8·1 (26·6)	7·0 (22·7)	12·4 (40·7)	11·0 (36·1)
Basal area, m.^{2} (h. sq. ft.)	22·8 (77)	20·4 (69)	22·4 (76)	20·7 (70)
Volume m.^{3} (h. ft. ac.)	102 (1122)	79 (869)	156 (1716)	136 (1496)
Form-factor	0·550		0·565	0·600

From the second trial with the same hybrid (S.210) at the same age, in an interplanting of one hundred of the hybrids between European larch of the same age of the "Sudeten-type", specially popular in the locality, a superior growth by the hybrid was again realized. They were planted as alternate plants in alternate rows of the "Sudeten larches". A measurement made seventeen years after the planting gave a height of 11·8 m. (38·7 ft.) and a diameter of 16·5 cm. (5·18 in. Q.G.) for the hybrids remaining, whereas the corresponding figures for the "Sudetens" were only 11·4 m. (37·4 ft.) and 12·5 cm. (3·92 in. Q.G.). Moreover, two hundred hybrids were put out with plenty of space between Norway spruces, and here, at an age of fifteen years after planting, the hybrids were 11·9 m. (39·0 ft.) high and 17·3 cm. (5·43 in. Q.G.) in diameter. At the time of measurement there were 197 of the original two hundred trees planted out surviving. On yet another site a similar two hundred plants had been subjected to repeated thinning, so that at fourteen years after planting only eighty trees had survived, which had a height of 12·5 m. (41·0 ft.) and a diameter of 16·5 cm. (5·18 in. Q.G.).

At the same time the hybrid (S.210) has been tried out on several other sites in small groups, and these have displayed vigorous growth. If we confine ourselves to what has been recorded in the above table only, the productive capacity of the hybrid strikes one as being much superior to that of European larch.

A comparison between the hybrid of Japanese × European larch and both the parent species, on the basis of controlled pollination and a known close relationship, can be made, with a little older material, only for some small lots. After pollination in 1933 and planting out in three small groups each of about one hundred plants, the following information may be quoted:

	2 Years in the Nursery	Measurement in 1942 (5 years after planting)	
	Height cm. (in.)	Height m. (ft.)	Diameter cm. (in. Q.G.)
European larch (S.140). Seed from free pollination of one good tree in a good stand	22·6 (8·9)	5·4 (17·7)	7·3 (2·29)
Japanese larch (S.127), V.425 × V.424	32·3 (12·7)	5·2 (17·1)	7·2 (2·26)
Japanese × European larch (S.126), V.425 × V.44	37·5 (14·8)	6·2 (20·3)	8·7 (2·73)

Because of a heavy and irregular felling carried out after the measurement was made in respect of selected " individuals for breeding ", no figures can be given for subsequent growth. What has been stated, however, indicates a considerable superiority of the hybrid in comparison with both species.

Now it has to be remembered that the material is very limited, and that we cannot expect to find a simple expression for the growth-vigour of the hybrid in relation to that of the parent species. This also applies to the relationship between the two species. There can be admirably planned comparisons between sample-plots, but we must at the same time remember that the result so obtained only applies to a material with the genetical attributes present in these circumstances. With hybrids and some other material, which have been produced by controlled pollination amongst a few individuals, the differences become even more conspicuous.

There is some evidence of difference between hybrid larches of various origins in a twelve-year-old experiment. Amongst Japanese larches related in the first degree (S.127), three specimens were pollinated with one European larch (S.140^4), and furnished in all about one thousand plants (S.555), whereas four other plants of the same closely-related lot (S.127) were pollinated with another European larch (S.140^1) and furnished three thousand plants (S.556). The two fathers were related in the second degree and selected as valuable forestry trees, but with a distinct difference in leaf-fall, which also showed up clearly in the two progenies. The controlled pollinations were done in 1941, sowing in 1942, and planting-out in the forest as two-year-old plants.

The two thousand " surplus " plants of S.556 were planted out on an area close beside the Forest Experiment Station's planting experiment 108 with sixteen different provenances of European larch, all similarly planted as two-year-old trees, but five years previously. The hybrid larches (S.556) have grown to be specially fine and at an age of twelve years are 8·1 m. (26·6 ft.) in height and 8·1 cm. (2·54 in. Q.G.) in diameter. The area is 0·23 ha. (0·57 ac.), and reduced to a basis of one hectare (acre), the basal area of the stems is 20·2 m.^{2} (69·5 h. sq. ft.). As their form has constantly been excellent, this would indicate that this is a valuable hybrid.

By way of comparison, where on another site it has been planted out along with S.555, the former is superior. With alternating use of the two sowings in lots each consisting of about forty-five plants and with two replications of both S.555 and S.556, the following results were obtained at twelve years of age:

Sowing	Height	Mean Height	Diameter	Mean Diameter
	m.	m.	cm.	cm.
555/42 .	7·8 7·7	7·8	7·5 7·0	7·3
556/42 .	8·2 9·2	8·7	8·0 8·1	8·1

In the assessment of this experiment no felling had previously been carried out, whereas in the previous case, with the trial of the same age of S.556, thinnings were made before the measurement recorded here.

Amongst other species crossings that of *L. Gmelini* × *leptolepis* (S.124, see p. 179 above) in a small twenty-year-old group gives the following result: pollination in 1933, seventy-seven plants planted out at 2 × 2 m. (6½ × 6½ ft.) in the year 1937; in December 1954 there remained twenty-eight trees with a mean height of 13·2 m. (43·3 ft.) and a mean diameter of 17·3 cm. (5·43 in. Q.G.). Other hybrids, like *L. Leptolepis* × *Gmelina* var. *olgensis* (the latter identical with " Korean larch ", seed of *L. Gmelini* received from Korea in 1915), S.209, which was produced in 1935, and *L. decidua* × *sibirica*, the mother of which was V.44 and the father a Siberian larch in the Forest Botanical Garden (S.519) produced in 1940, and other later ones seem promising. These are only examples of many possibilities, and they must inspire us to make further use of them under local conditions.

Although the experience we have concerning species crossings, which have been produced under control, has as yet extended over a period of time of only about twenty years, it nevertheless gives us grounds for optimism. There is also the possibility, however, that something of value may be realized through F_2 or back-crossing from the hybrid to the pure species. As the material for this must also rest upon controlled pollinations, it is necessarily still younger. To illustrate this problem only one report, of some material about ten years old, will be given here.

It consists of ten progenies derived from pollination in the spring of 1942, sowing of the seed in 1943, and planting-out of the plants in 1945 and 1946 in groups of one hundred to two hundred trees of each. Concerning the basic material reference may be made to the previous description (p. 179), but it may be recapitulated thus:

European larch: V.44 (Fig. 1) and S.140 (related in the second degree).
Japanese larch: S.127 (related in the first degree).
The hybrid Japanese × European larch: S.126 (V.424 × V.44).

The figure appended as a coefficient to that standing for the sowing is an indication of the number of the tree in question within the sowing.

By controlled pollination in 1942 the following were produced:

Pure species:
European larch:
S.635 (S.140^2 × 140^8)
S.640 (S.140^7 × 140^8)
Japanese larch:
S.627 (S.127^{11} × 127^2)
S.626 (S.127^{10} × 127^2)

Back-crossings:
F_1 × European larch:
S.641 (S.126^7 × 140^8)
S.646 (V.44 × S.126^1)
F_1 × Japanese larch:
S.645 (S.126^8 × 127^2)

F_1 and F_2 of Japanese larch and European larch:
F_1:
S.631 (S.127 × 140—three trees of S.127 and mixture of pollen from several trees in S.140)
F_2:
S.643 (S.126^6 × 126^1)
S.642 (S.126^5 × 126^1)
(S.644 (S.126^1 self-pollinated))

Even in the nursery there were considerable differences. The planting-out was therefore distributed over two years in order to get plants of approximately the same size for putting out in the forest. After planting, all the lots have been thinned twice; the first time by taking away every other row, and the second time by removing every other plant. No selection has thus been made, although the number at the last measurement refers to only a quarter of the plants originally put out.

As is evident from the summary, attempts of several kinds have been made to maintain a close relationship between the pollinators in order to make various comparisons and analyses possible. Leaving these details out of account, however, only the curves based upon height measurements at the ages of two, four, five, eight, and ten years will be given here (Fig. 61).

Measurements of the heights brings out the interesting phenomenon that, broadly speaking, the order of growth follows the same sequence at an age of two years as at the last measurement at ten years, and that the difference has steadily become more pronounced. This means that one can with some confidence draw conclusions about how such a material will develop when it is still young (cf. Fig. 49).

Amongst the various crosses, F_1 deserves attention. It lies well ahead of all the other pollinations carried out, whereas the pure species lie last. The intermediate material is by no means poor, however, and it displays such vitality that it merits considerable attention. It is possible that in this way valuable results can be achieved because of wide variation within the individual progeny and by the particularly fine growth of a small number of individuals. This must not be left out of account, although the idea which first strikes one would of course be to raise the best possible material of the two pure species and produce F_1 from that for use in forestry by means of a seed-garden.

The behaviour of the larch in respect of *disease* is of at least as great importance as the phenomena pointed out above, and in this connection also some experience has been gained. As examples two experiments may be mentioned, of which one refers to *Chermes* and is elucidated by the use of clones, whereas the other refers to the very harmful *Dasyscypha Willkommii*, in respect of which the observations were carried out on seedlings.

In growing close beside one another three clones of *L. decidua* (V.44) and *L. leptolepis* (V.45) respectively and one clone of the hybrid V.44 × V.45, a heavy attack by *Chermes* occurred on V.44 and V.44 × V.45, whereas V.45 was quite untouched. The susceptibility was thus transmitted from a plant of *L. decidua* to the selected plant of the hybrid. The experiment was intensively reported previously on p. 118). Here we shall merely repeat that severe pruning very greatly promotes attack by *Chermes*, so that by using it in combination with clones it gives us a technical aid in testing selected breeding trees.

A tree may be susceptible to attack by *Chermes* without its being possible to observe it upon the selected tree, when it perhaps stands under favourable

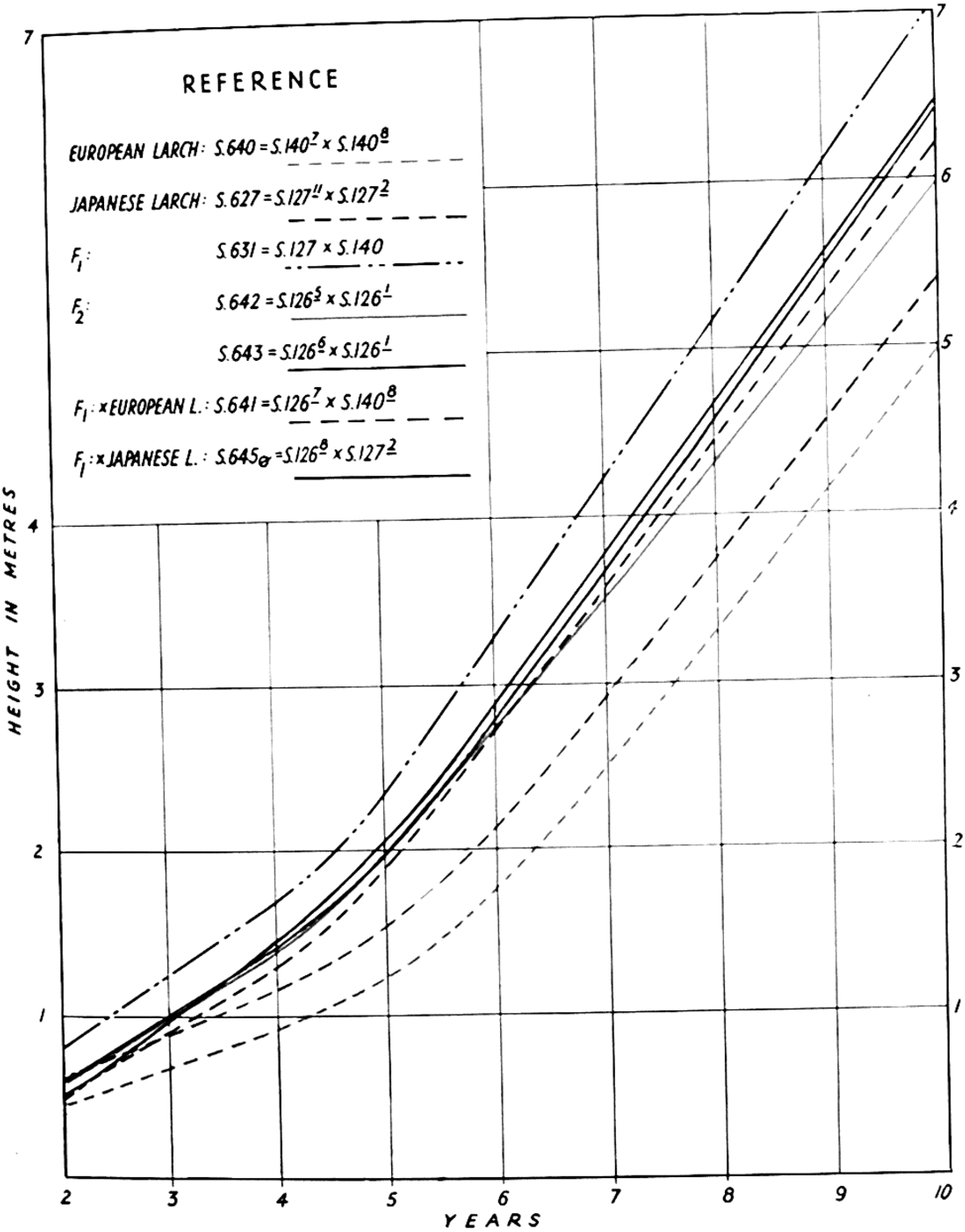


Fig. 61. *Larch*. Controlled pollinations, sown in 1943. Height-curves for seven samples. Drawn on the basis of measurements in 1945, 1947, 1948, 1951 and 1953. Note the superior growth of the F_1 and the close agreement in the order of all samples.

conditions in the forest. It is an attribute, moreover, which seems to be liable to much variation even within a species rather severely susceptible to attack, like *L. decidua*. It is therefore a factor which is not without significance in choosing trees for breeding.

In the north-west of Europe, where both European and Japanese larches are exotic tree species, *Dasyscypha Willkommii* is usually present on the European larch, whereas the Japanese larch is generally considered to be resistant. It is likewise claimed for the hybrid that one of its greatest advantages is pronounced good health. In order to throw more light on this, and in particular to get some evidence of whether this is a question of a genuine resistance, or whether at most it has to be attributed to the fact that the hybrid does so well because of its vigorous growth, the following experiments may be considered.

As research material, plants were used of the two lots mentioned above (p. 189), S.555 and S.556, which are both of Japanese × European larch. On one research area where larch had been grown over a number of years, and where it was strongly infested with *Dasyscypha Willkommii*, two small lots of both S.555 and S.556 were planted out. Both sowings were grown on a particularly unfavourable site and on a rather well-suited site respectively. On examination throughout the years up to an age of twelve years, attack by *Dasyscypha* has been found on all four samples. While it was clearly observable on both of the unfavourably located plantations, it still occurred, but weakly, on the two better-placed groups, and right from the start it has always been most severe on plants of S.555. It has not been possible to prove with certainty that plants have died for this reason. To all appearances the attack has had the character of an infestation on branches and on branch bases. On that lot of S.555 located on the unfavourable site the attack was so strong that it caused damage to several stems. On the more favourably situated lot of S.556, from the forestry viewpoint, the attack was found to be slight.

This should be looked at in conjunction with the fact that, during the above-mentioned (p. 190) trial of these two sowings under normal forest conditions, from a careful examination of the plants at twelve years of age, a weak attack of *Dasyscypha* was found on suppressed dead branches of S.555. Up till that age all the plants in the experiment of both S.555 and S.556 survived; in spite of this it was not possible to find the fungus on even dead branches of the more vigorously growing S.556. To this it may be added that neither was it possible to find any attack on the group, also mentioned above, of the original two thousand plants of S.556. Because of the thinnings carried out in the latter, the larches in it have also enjoyed a satisfactory environment.

It may be seen from this that the hybrid Japanese × European larch can be attacked by *Dasyscypha Willkommii*, but that there may be differences between the various progenies. S.556 is, for example, more resistant than S.555. The hybrid is not really resistant to the fungus. It has occurred on hybrids which have been placed under conditions specially unfavourable for the well-being of the larch.

We have also seen, however, that under the most difficult conditions the hybrids have been capable of making a heroic struggle against the disease. The battle between the larches and the fungus has been waged, moreover, under such difficult conditions that it would for other reasons not be possible to expect a satisfactory yield from growing larch.

The cumulative evidence is that it is true, as J. M. MURRAY had already announced in 1915, that the resistance of the hybrid must essentially be attributed to its vigorous growth. "It is true fructifications of *Dasyscypha* have been found on the stems, but, probably owing to rapid growth of the trees affected, no cankers were formed."

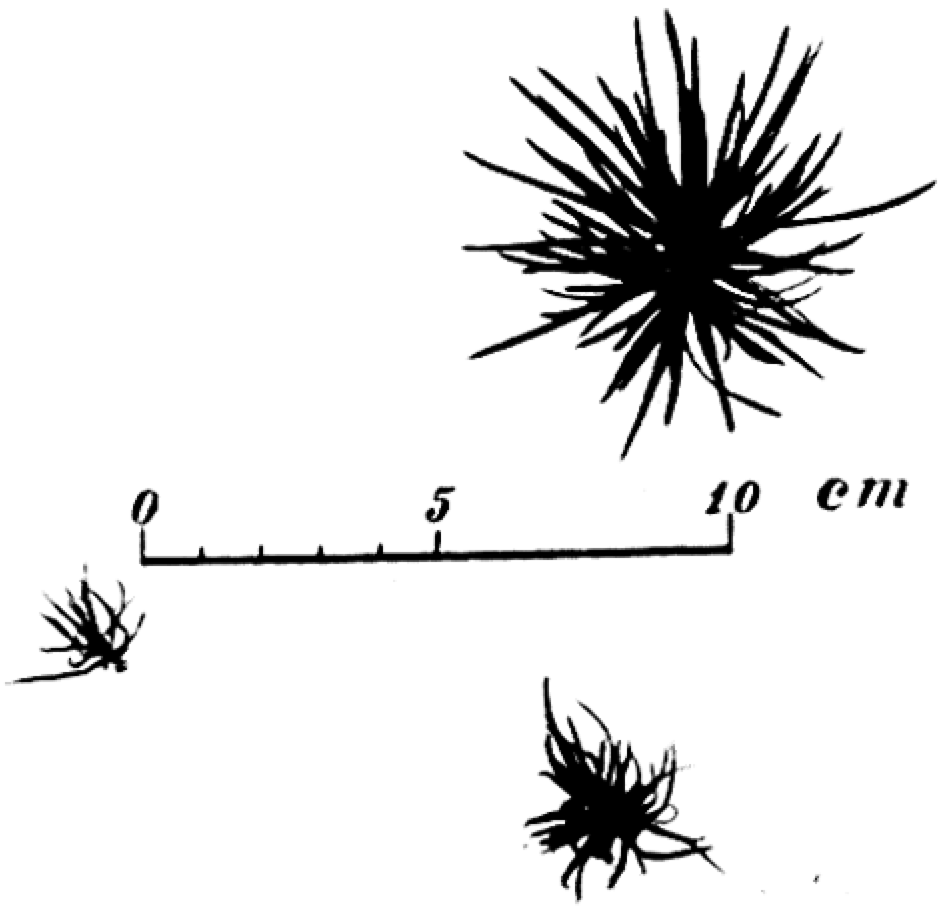


Fig. 62. *Larch.* Progeny from pollination between diploid and triploid larches. S.127[3] (diploid *L. leptolepis*) × S.21 (triploid *L. decidua* × *occidentalis*). Sown on 11th May 1942 and photographed on 17th October 1942.

With the help of *cytology* progress has been made to the extent of having both a triploid and a tetraploid larch incorporated into breeding work. With the knowledge which we have had for the past twenty to twenty-five years respecting the cytological conditions in coniferous trees, this is really surprising. That it has not as yet given any practical results is quite another matter, but there is sufficient to give encouragement for further work on these lines.

Fig. 62 shows the great variation in progeny from pollination between diploid and triploid larches. The opportunity exists of getting new tetraploid plants in that way; along with the tetraploid plant already discovered they would be valuable material in any future breeding.

Improvement through inbreeding also attracts attention. By the use of species-crosses definite results have been achieved, which must primarily be regarded as the outcome of heterosis. The obvious thing to do is to try to increase this effect through previous inbreeding, and to pass on to the use of heterosis in the case of pure species through inbreeding of types.

There are reliable results in respect of vigorous progeny derived from controlled pollination between both trees related in the second degree and those related in the first degree. Similarly, there are so many controlled instances of useful progeny after self-pollination, that there is very great encouragement to endeavour to make use of them technically.

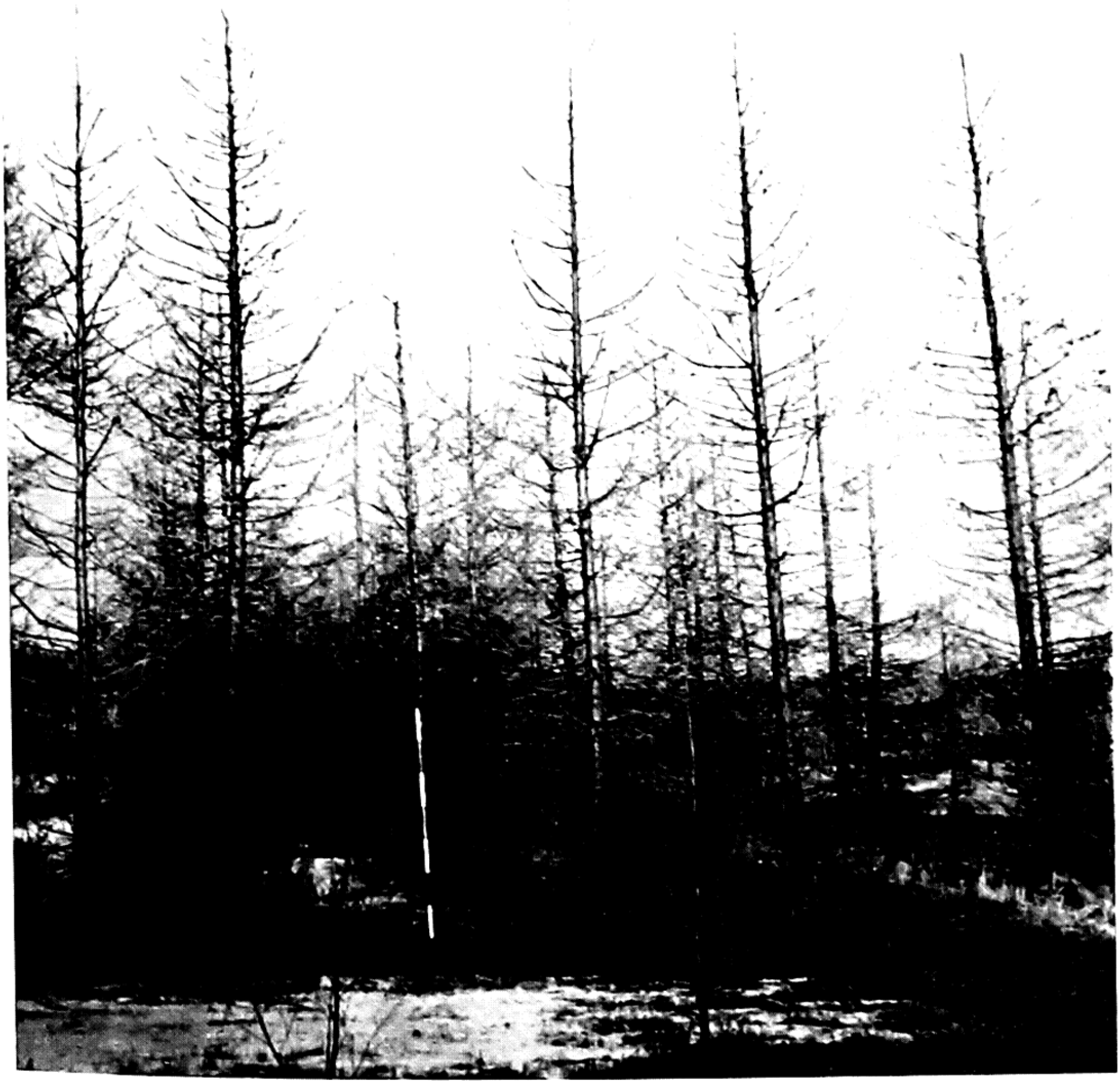


Fig. 63. Inbreeding. S.648. Progeny from self-pollination of the fine larch in Fig. 1; performed on the graftings in Figs. 2 and 3. Pollination in 1942, sowing in 1943. Photographed in January 1955.

There is a risk, however, that after a few years a beginner may lose hope of being able to progress on these lines. It is not unusual for these plants raised by self-pollination to display in the early years a noticeable inbreeding depression. If such plants are planted out under the same external conditions and at the same age as other plants produced by normal cross-fertilization, the self-pollinated ones will find the conditions all too unfavourable and will readily disappear. From that, one may reach the conclusion that this is evidence that self-pollination is of no use. That is quite wrong. In several cases it has been demonstrated that if these plants which grow weakly in the early years are carefully looked after, they may later grow up into specially useful plants. We must be very much alive to this and not give up too soon.

Through self-pollination one first of all gets some idea of the genes contained in the individuals used. As an example, it may be mentioned that the oft-quoted *L. decidua* V.44, by repeated self-pollinations of the tree over the years, has given a very promising and rather uniform progeny. Amongst the progeny derived from free pollination a specially large and vigorously growing plant has given by self-pollination a likewise vigorously growing but coarse lot of plants varying a great deal in form. The most slender plant, likewise derived from V.44 and thus a half-sister of the foregoing, gave predominantly slender forms. The latter progeny is the subject of further inbreeding and has given plants both by pollination from related progeny of the first degree and by fresh self-pollination.

By similar methods of procedure in Japanese larch, or whatever one happens to want to cross with, and by reproduction in clones of the individuals selected in the first and subsequent generations, material is obtained for future seed-gardens.

The work takes a long time, so that there may be a temptation to seek a short cut, which could at least be used for preliminary investigations. In order to find such material we must go to single individuals of the species, such as are found, for example, in botanic gardens. There one may be successful in finding the occasional tree which has been isolated as a " rarity ". The local gardener has also now and then taken seed for his own use or to exchange with other botanic gardens, so that it is well worth while to study such collections a little more intensively.

As an example of the use of one such self-pollination found by an accident, the following may be quoted about *Larix Gmelini*. A tree planted in 1890 stood in our Forest Botanical Garden in such a way that it was reached by pollen from a *L. leptolepis*. The greater part of the progeny were hybrids, but in a more exactly studied progeny from 1918 there was found to be a small number of rather small plants which could only be presumed to be self-pollinations of *L. Gmelini*. From one of these plants we now have a plant which is called S.95, and can be explained only as a new self-pollination. Plant S.95, which was sown in 1933, is a remarkable fellow. It is not a very large and elegant tree, it is fairly slow-growing, but, like the mother and grandmother, it flowers very abundantly with both female and male flowers.

Self-pollination of S.95 gives an abundance of plants. They are certainly slow-growing but nevertheless quite vigorous enough, and although they are still only young, yet they are remarkable for a striking uniformity. In this progeny of 585 plants (S.1553), there have not been found any characters other than those characteristic of *L. Gmelini*.

By open, uncontrolled pollination of S.95 we get quite different strongly growing plants. The tree stands in an experimental plantation surrounded by very different larches. It is very exposed to open pollination from *L. decidua*, *L. leptolepis*, *L. leptolepis* × *decidua*, *L. Gmelini* × *leptolepis*, *L. laricina* × *decidua*, etc.; this gives the young progeny (S.1554) a variation of

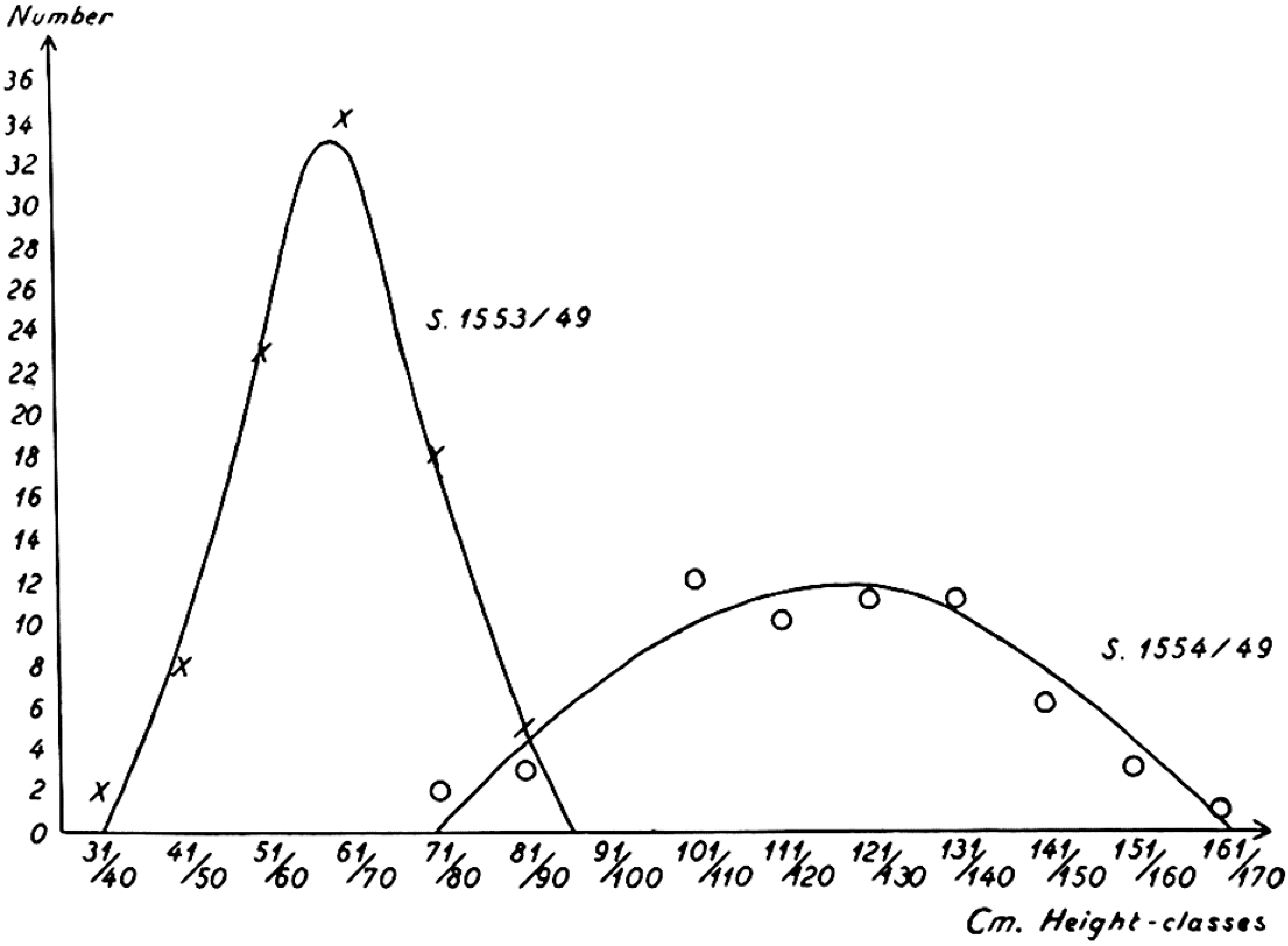


Fig. 64. Distribution of height-classes in cm. of S.1553/49, which originated by self-pollination of a larch, which is itself believed to represent the second inbred generation of a *Larix Gmelini*, and of S.1554/49, which originated by free pollination of the same larch. The 3-year-old plants were measured in November 1952.

bark colour, but no attempt can be made to unravel who the father may have been; nor is that of interest. The important thing to note is that the progeny as a whole consists of vigorously growing plants.

Of the two progenies, from self-pollination (S.1553) and from free pollination (S.1554) respectively, one lot of each was picked out for careful tending, in which sorting or anything like that has been avoided. After their third year in the nursery they displayed a striking difference in size; this is illustrated in Fig. 64.

Although research and our own knowledge of the use of self-pollination in breeding forest trees is still modest, yet it is very encouraging. We shall therefore end this chapter on the breeding of larch by repeating the words of MOGENS WESTERGAARD quoted in Chapter X on p. 171: It can scarcely be doubted that the heterosis method is the answer to breeding difficulties due to cross-fertilization. In fact it eliminates entirely the two unsolved problems, determination and fixation of the good genotype.

CHAPTER XII

BREEDING AND MECHANIZATION

THE setting of present-day technical development is an ant-like diligence employed in "analysing" the material with which nature has provided us. With primitive implements from these simple elements increasingly better tools have been placed in our hands. Everything to-day depends upon the marvellous developments in steel and oil.

Whether we admire or fear it is very much a matter of indifference. We are all dependent upon it—and it is certain that if rendering the earth fruitful by way of agriculture and horticulture had not kept pace with this development, there would have been fewer of us to enjoy the goods. Things have not gone quite so far as that.

Agriculture, which is essential to man's mastery, has won from nature soils, plants, and animals. Man has cultivated and improved not only the soil, but also the plants and animals. We are now at the stage of bulging crops, which is based upon a use of the soil through a combination of implements, of manure produced in factories, and of breeding of plants and animals.

We are so far away from the first primitive improvements, both of plants and of domestic animals, that it is quite often difficult to recognize the connection between the present-day products and the original elements. In this connection, however, one must not, of course, be lured into believing that breeding alone could have brought about these advances. None of the three factors—equipment, manure, and breeding—could have done it unaided. They were intimately linked together. One is dependent upon the others and all three have supported each other on the forward path.

Plants and animals must have genetical attributes of such a kind that they can "give a return" for artificial manuring and concentrated fodder. The primitive motor runs on cheaper and cruder fuel than the engine of the newest model. If we go to the expense of the dear and powerful fuel for the modern motor, the result will be satisfactory. The primitive motor, on the other hand, does not provide greater power with the costly fuel, even if it is able to put up with it at all. To-day we have large and valuable bacon pigs at only six months, when they have been kept in the sty and had the right food. Almost two hundred years ago pigs in this country mostly ran free and, generally speaking, had to procure their own food. They could then be slaughtered at an age of from two to three years, but they had been cheap to feed. Now, tending, food, and animals are all different from what they were in those days.

Agriculture and horticulture have been able to keep pace with the technical development and have contributed in advancing human society to its present state. It is extraordinary that forestry has remained standing at a level which is in many respects primitive. Although it is true that we can speak of a civilized forestry, in which great advances have been made by proper planting and tending, yet nevertheless, upon the whole, we utilize the trees much as they have been given to us. Although we also boast about increased production and quality, which have been achieved by the use of exotics and, still better, by the use of types which have been discovered by experience through provenance trials, yet nevertheless to-day one easily recognizes the original trees. It is only like a drop in the ocean and it applies equally well to the forestry of long-settled countries and to the uniform plantations of teak, eucalyptus, or conifers of recently settled lands and to the " tree-farms " in the U.S.A. and Canada. On the whole we are cultivating only those same trees which were at the disposal of our remote forefathers.

Man has also throughout the ages driven the forest very far back. Mankind had to use much space for the necessary, but in ancient times primitive and space-demanding, farming. The forest was looked upon as an enemy and ravaged and burnt wherever one could most easily get at it. Much extremely valuable forest has had to be cleared, by which valuable inherent tendencies (genes) may have been wiped out, which will be greatly missed when the forest has to be cultivated. From the point of view of future forest management alone—the cultivation of the tree-species, which is bound to come—it would be good business to protect and preserve for the future the most valuable trees and remnants of forest associations. Cf. p. 37 above, about the trees in their optimum.

Seen against the background of the sins of the past, all over the world there are great projects for checking erosion, destructive floods, advancing steppe formations, for constructing shelter-belts against blowing sand, and much more. For this a demand will arise for material bred for these specific purposes, produced from the hardiest and most effective individuals. There will be still greater need, however, for timber production, which is essentially of economic importance.

We have neither the time nor can we afford to leave things as they are. The fact that " cultivated " forestry occupies the position it now holds is most certainly not due to profound deliberations. We have been forced into it and there have been many reasons for that.

First of all, the remaining tree reserves have been discovered to be so immense. Thanks to technical developments we have also such wonderful equipment for knocking the forest down. We have bull-dozers for making roads and splendid lorries for transport, so that mills can work larger and larger territories. One readily gets from that a feeling of wealth and power —but we have also blindly looked upon the *methods* of breeding in agriculture as the only ones possible for improving our trees. It is the interplay between these things which has in the first place reassured us, and in the second place induced us to let things slide. If we were to follow the methods of working in agriculture, our breeding would require such a length of time that it would not be comprehended. The most that one could hope to get would be a more valuable material by using species or types from another geographical region. One would not dare to go in for raising anything, for " constructing " anything new and better, although one would like to be up-to-date and would, of course, talk a good deal about genetics and improvement.

I make so bold as to call this primitive, and we must struggle to raise silviculture to a higher level. Agriculture and horticulture do not allow themselves to be satisfied with what the community deals out to them in the shape of land. They choose it themselves and leave the poorer areas alone. The farmer has long ago discovered that the cost of growing good food for his animals pays, although he could perhaps get the food gratis on grazings that are difficult of access. It is the same with the gardener, who in North America spends much money in growing improved bilberries, although like the Indians he could pick blue-berries gratis in the forests. We foresters, on the other hand, pay steadily increasing sums in exploiting the growing-stock of timber provided by nature, although it becomes more and more difficult and expensive to reach. This applies to both the far north and to the tropical and sub-tropical rain-forest.

We have to grow timber. We have to look out where the forest-areas of the future are to be and that means where it will pay us to grow trees. The trees should attain their finest growth, and the production, with the smallest expenditure, should be able to go straight into saw-mill and factory. To say this is not to under-estimate in any way the important task of growing forests as a protection for agriculture and other land-uses. Because of the social importance of forests there are in a great many countries laws to protect them, but we should not merely live under the protecting wings of these laws. We should be aware of our responsibilities and attentive to the various functions of forestry, one of which is to build up timber production economically.

The area and its situation are important, as timber has a high " accessibility value "; transport is costly. We must not, however, under-estimate consideration of light, warmth, and water. Those regions of the globe which are favoured in this respect will have great advantages. To-day, forests are being exploited in the far north, for large reserves are still preserved there, and because they consist of a " uniform commodity " of few species, and these all conifers; but it is definitely not because the trees grow best there. Far from it. It will in future be regarded as unadulterated mining, which is simply due to the large growing-stock which has accumulated there. The production which is economically correct we achieve by arranging for light, moisture, and warmth. If we cannot do this on account of our national limitations, we must to a much greater extent than hitherto go in for improving the material; but why not do both things? It must be the aim of all of us to plant only that tree which it can pay us to harvest.

There is not sufficient evidence for the " inexhaustible timber supply ", which is only careless talk. Although the accumulated growing-stock at this moment might even last for several generations ahead, it is nevertheless far from certain that it will be economically sound to exploit the possible yield. There is such a glaring contrast between the present difficulties of getting timber of the quality and quantity desired as compared with the position only one or two generations ago. Moreover, it is certainly the general opinion that wages will rise, and if timber consumption should expand only a little further at the same rate as in recent generations, then there is not the slightest doubt that, as foresters, we must do something drastic. We should not be pessimistic and despondent, merely advising that felling of the forest should be restricted. We should fell what there is a use for, while at the same time contributing with all our might to the best possible exploitation of the remaining forests, and similarly we should throw ourselves with optimism into a bold offensive to construct new forests.

As sensible workers and fighters we must then look to our tools in advance. Although they are primitive, they are not unserviceable. Let us first examine them in relation to those of the " favoured " agriculture.

The most striking difference is without doubt the speedy succession of crops in agriculture in contrast to forestry's long-term production. In this connection it must be said, however, that the farmer not only *can* harvest every year; he *has* to harvest every year, no matter whether the prices and the costs are up or down. The forester, quite otherwise, can vary the harvest according to the market demand. This is true both of the final yield—the main felling—and of the thinnings taken out as intermediate fellings. With rising labour prices the farmer has each year rising expenses, and his only hope is an increased yield by increasing the use of manure and progress in breeding. With the same assumption of rising labour prices, the forester obtains an increasingly more valuable forest because his outlay was incurred at a relatively favourable period.

It is very doubtful, moreover, whether the rapid succession of generations of the herbaceous plants is of itself an advantage in breeding. It is certainly true if we follow the customary procedure of agriculture in breeding; but the aim of the preceding chapters has been to satisfy ourselves that there are other ways of working. Instead of sighing over the slow succession of generations, we can with just as much reason reverse the problem and stress the advantages when dealing with long-lived individuals (" breeding animals ").

For the annual plants the genetical attributes are preserved from one year to the next, from crop to crop, only through the seed, that is, only through the sexual generation with its unending opportunities for genetical alterations. In most cases the farmer lacks entirely the opportunity of preserving the outstanding individual unaltered, by means of vegetative propagation. Our tree-shows will soon be an object of envy, for not only will they be displays for judging between individuals, but they will also be exhibits of the most outstanding trees brought together in the course of time, which are kept alive for constant use.

Where vegetative reproduction is so difficult that it does not allow of an easy and certain preservation of the unaltered genotype, the rapid succession of generations also means that improvement must be carried on like a ceaseless contest. There are opportunities for advancing every year, but also for falling back. In any event a great deal of expensive apparatus has to be maintained. Breeding in agriculture may be compared to advancing along a smooth but uphill slope. Plant-breeding in forestry is better compared with travelling up a staircase. For each advance we make we go up one step; but, thanks to the ease with which we employ vegetative propagation, we stand thereon securely. We can pause for a rest on this step and gather our forces to take the next step. It is very likely that the steps in the staircase are not equally high, and they may become more difficult as we ascend. At the moment, however, they are easy to mount, as much experience shows, of which an account has been given earlier. The future difficulties remain unknown to all of us, both farmers and foresters. One or two things, like improvement through heterosis and combining ability, which represent something very new and most promising in agricultural breeding, are even easier in forestry. They are, so to speak, made for our long-living " breeding trees ".

We can very comfortably begin our climb up the staircase; we are no more likely to become dizzy than the farmer. The staircase may have high and difficult steps, but we can take a good rest in advance. The smooth way up the slope may also have slippery lengths, which may be smooth and difficult to surmount. There are various routes upwards, but it is not possible beforehand to say that one is more favourable than another. We foresters have been allowed to use the staircase only—and even then we have hesitated all too long.

Nor must it be forgotten that our aim is different. Agriculture almost everywhere makes in a sense very exacting demands upon uniformity. We are not troubled with that. Crops in forestry are perennial associations, in which there are harvests at various times. In them, as in other societies, there is a considerable advantage in being exempted from having to say who constitute the best type of " citizens " and allowing them to reign alone; our only demand is that all of them, each in its own way, should be valuable members of the community.

In assessing the value of the genotype there is some inconvenience with trees which live long. It was mentioned above that the long span of time, which elapses from the birth of the tree until we see it as a mature and valuable tree in the forest, makes it difficult to select *élites* immediately. The appearance of the tree is a product of the inherited tendencies and the environment, and as the latter has had leave to operate particularly long and intensively in old dense stands, it must be presumed to have special significance. It is often stressed as being something unfavourable—something which places plant-breeding in forestry in a worse position than the work on agricultural plants concentrated in rows and lines.

That is not quite true. In the first place we have our tree-shows, which help us very considerably to follow the trees " from the grave to the cradle ", instead of the usual way from the cradle to the grave (cf. p. 111). Instead of speaking about " the effect of the environment " and regarding it as something of which no use can be made, we must change this to speaking of its " training value ", and look upon it as a means for improving the material. Such an attitude also involves our being able to throw ourselves boldly into breeding with the main object of obtaining vigorously growing individuals, well equipped to meet disease and capable of being " trained ". It is possible that we can discover or raise strongly growing, healthy trees which are, at the same time, of excellent form, which may stand at a wide spacing and make full use of the light. It is by no means an exorbitant demand that all three factors should be controlled simultaneously. Forestry can profit by " training " to a greater extent than agriculture.

Finally, we must not run any risk of a loss of growth-energy, from an excessive anxiety that the trees, by their own propensity in accordance with their content of genes, should not be well shaped. The strongly growing tree can, by its branch formation and demand for light, become a good citizen working economically in a crowded community, although in an isolated position it might appear less attractive. The status of the problems is in many ways different in forestry from that in agriculture. Above all we must not allow ourselves, from a consideration of what agriculture demands, to be led to believe that we have experience in these matters, and proceed with too restricted and too hasty a choice of contents for our " seed-gardens ". Provided we are reasonable and remember the essential differences between agriculture and forestry, we also shall reap great benefits.

All the difficulties do not lie with forestry, nor is the contrary by any means true. Difficulties confront both professions, and this deserves to be stressed, for forestry is so often described as being faced with such difficulty in its plant-breeding. Nor is it so very strange that forestry should have encouraged such an idea, for we have need to make excuses. It is the primitive position of forestry in this field that has been the limiting factor for a more intensive cultivation of trees, for a highly developed silviculture. Our planting material is differentiated so slightly from that provided by nature that progress in silviculture—increased production through managed forests—has had to be brought about almost entirely by more careful planting and thinning.

Recommendations that there should be a production of better seed—an improvement of our forest trees—vary a great deal, depending upon the local situation prevailing in forestry. In districts with highly developed forestry which is based solely on artificial sowing and planting, or in districts where it is a question of planting up new land (afforestation), every single opportunity will at once be seized in order to obtain the genetically best plant material. That is self-evident, for it costs just as much to plant good plants as bad. Even with a modest use of the breeding methods described above, it will be possible to advance rapidly towards elimination of the poor types. It is one of the important points in forest-tree breeding not to waste time by reflections about the complex of genes that will be needed to arrive at the very best, but to set to work as soon as possible to get rid of undesirable (qualitative) genes. There is every hope that such rapid and important progress may be made in that way that it will not be long before the advantage will be realized of making heavier interventions, even in forest regions where there is plenty of opportunity for natural regeneration.

It is only twenty years since we in Denmark grafted our first ash for use in improvement. We were then in the position of having only forest botanical information that the European ash could flower by different sexes, over a range from pure female to pure male trees covering numerous distinctive combinations. We now have seed-gardens composed of graftings from the best female and male trees, so that they have made an appreciable contribution to supplying the forest with seed. This would be even easier in American species of *Fraxinus*, for example, which are more purely diœcious species (see p. 51). This and what has been said about the breeding of larch are only small and incidental examples of the opportunities which exist; some further considerations will therefore be mentioned.

It is a very characteristic feature of by far the greater number of forest trees, and one which must be stressed, that they do not furnish a regular annual yield of seed. It often happens that they are completely or almost completely devoid of seed for more or less long periods of years, between which years occur with overwhelming seed-setting. Since at the same time the seed-setting of the individual species varies with the climate in which it is growing, opportunities arise, during local seed deficiencies, to import seed of the same tree-species from another climatic region, and that has led to grave mistakes. As tree-seeds during ordinary storage tend to lose their germinative capacity rather quickly, it is important to employ a careful method of storing quantities of suitable tree-seeds when they are abundant in order to avoid deterioration in the quality of the stands being established. In order to profit from breeding, our first requirement is to have our equipment in order for storing seed to distribute over the barren years. Secondly,

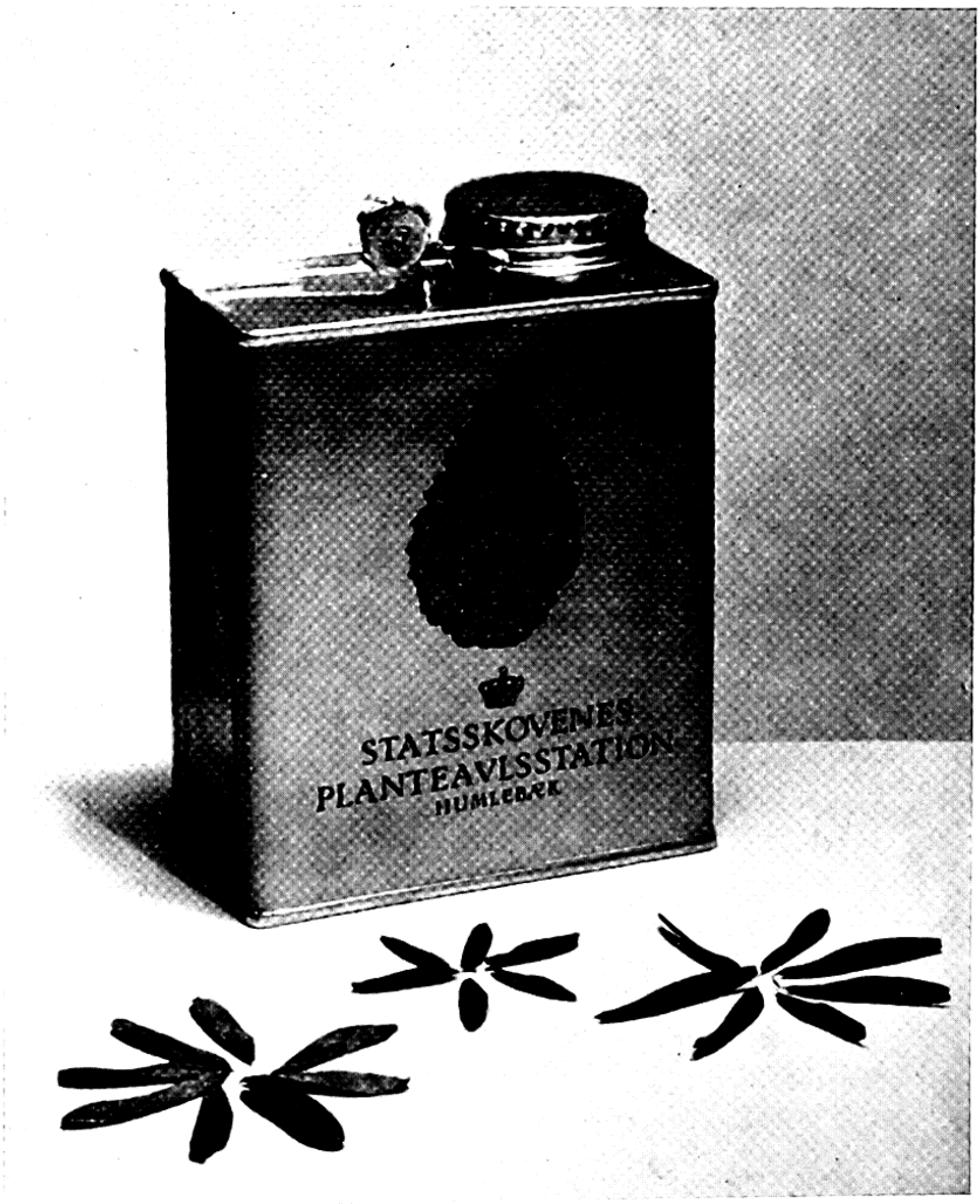


Fig. 65. Seed-box from Seed Extracting Plant, Tree Improvement Station of the Danish State Forest Service. At the side of the box seed from three selected trees of *Fraxinus excelsior*. Note the individual differences in seed morphology, which makes effective seed control possible.

production of seed must be kept quite separate from production of timber, so that we can get our store filled with seed from seed-gardens constructed for that purpose.

An essential proviso is that the species in question should display sufficient individual variation, and that seems to be the case with our forest trees. On first thoughts one might be inclined to think that the " important " species with the greatest geographical range are the most variable. Such an idea might be strengthened by impressions gained from the provenance trials of forest research stations. It must be remembered, however, that for such trials a special interest has been taken in the geographical variation (see above under " progeny trials "). Less attention has been given to the mutual variation within each progeny. In respect of variation in a tree-species, just as much attention must be given to the individual variation in the constitution of the tree as to the total variation of the tree-species in its relationship to the climatic conditions. Similarly, the tree-species in themselves seem to be very different in their capacity to endure, and indeed to benefit from, transfers to another climate.

Two trees of the same species may be very different in their structure. It is usual in this connection to refer to those very divergent forms which have been given special names, such as var. *pendula*, *fastigiata*, *nana*, etc. That is, however, tantamount to fastening upon what is negative to a forester. Looking at it from the opposite direction, we might mention here a tree, clone V.661, which shows signs of having a favourable structure from the point of view of economic forestry. It must be asked of such a tree that the leaves (needles) should

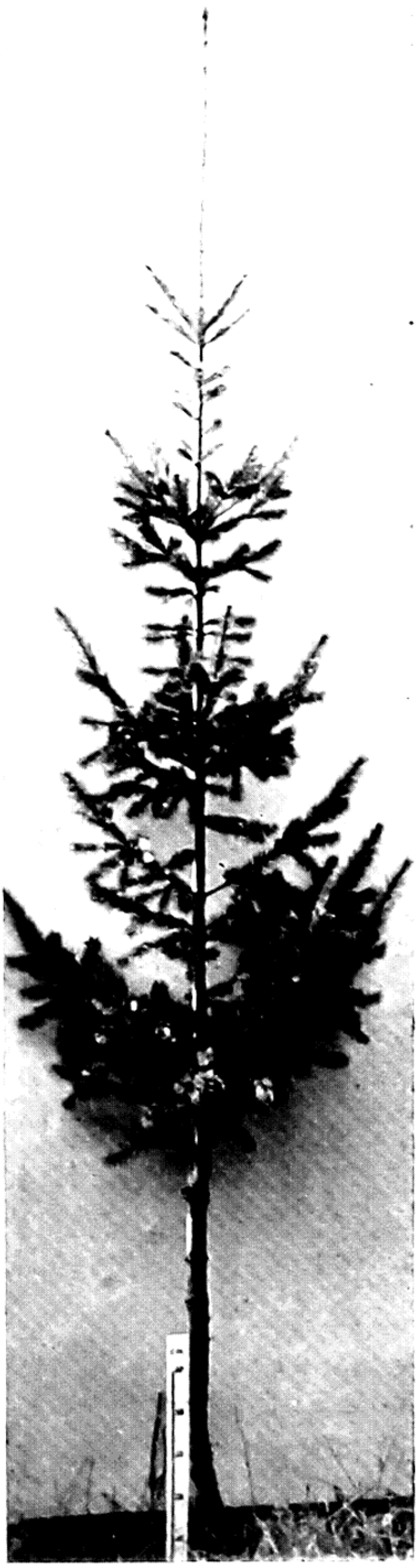


Fig. 66. *Douglas fir* (V.661). Selected from Linaa Vesterskov, Denmark. Grafted 1943, photographed 4th November 1949.

form such a mass and be so placed that they can give the plant the best possible capacity for growth, and further it should have the least possible amount of branches, and the greatest possible amount of valuable stem. (See Fig. 66.)

Clone V.661 is the vegetative reproduction of a strikingly slender and healthy Douglas fir. The striking thing about this tree is that with its slender crown and relatively fine branches it shows vigorous growth, and that the stem is keeping up a satisfactory rate of diameter increment. Like other individuals, this tree produces on the basis of its existing foliage a certain number of branches and a stem, but the ratio between these factors is very different. For V.661 certain dimensions are placed along with the corresponding dimensions for two other individuals, one of which is a clone of the same age, which has also been chosen for breeding but rejected later, and the other is a tree of rather ordinary but very good type from a young plantation of Douglas fir:

	Total Dry Weight of Needles	Total Dry Weight of Branches	Dry Weight of Stem
	kg.	kg.	kg.
V.661 . .	2·327 (38%)	1·451 (23%)	2·340 (39%)
V.657 . .	1·063 (31%)	1·163 (34%)	1·199 (35%)
Ordinary type	3·623 (40%)	2·527 (28%)	2·866 (32%)

From this it may be seen that V.661 has an astonishingly large amount of needles in proportion to the weight of branches. From the illustration the open growth of the tree may be seen, which provides the needles with a favourable position for utilizing the light; they do not shade each other. If the ratio between the amounts of branches and of stem produced is examined, the figures show a very favourable ratio for V.661. With by far the smallest amount of branches it is able to build up a relatively large stem, which from the point of view of forest economics is the only important part of the tree. It is therefore a valuable tree, as it has at the same time proved to be a specially healthy tree under the local conditions (see Fig. 43).

What has been said is only one example of how different from one another even very good trees may be as regards their structure from the forest-economics viewpoint. Many other factors enter into this question of quality, such as curvature of the stems, tendency to become cleared of branches, resistence to disease, etc., each of which is itself liable to variation, and which together give the multiplicity of individuals differing each from the other within the individual tree-species. This is such an important basis for the use of our tools that it must be dealt with in relation to a few economically important tree-species.

Douglas fir, *Pseudotsuga taxifolia*, is economically the most important conifer in western North America. Because of its excellent timber, vigorous growth, and capacity to grow in western Europe, many attempts have been made to elucidate the geographically different types of the species. Much progress has been made, and it is important to know from what region we should derive the seed for plantations in Europe; in the same way, in western North America itself, seed should not be taken too rashly from one region to another. On the other hand it is the more surprising that far greater efforts have not been made to get seed from the most promising stands, let alone from the best trees.

One has to travel very widely throughout the natural range of Douglas fir in order to get an impression of differences in geographical type, but standing on one place one can, without moving a foot, see many individuals differing widely in their structure; it is often more difficult to pick out those that resemble one another. Although they belong to the same species and the same geographical type, yet they can be widely divergent in respect of their economic value in forestry. This can be observed everywhere. It does not matter if one chooses in California a site in the Coast Range or in the Sierra Nevada, passes through Oregon and Washington, or in British Columbia selects a place on Vancouver Island or in the Rocky Mountains; everywhere one is bound to be impressed by the great individual variation of this tree-species.

Wherever tree-species do well, and where, throughout centuries, they have been able to grow untouched by man, one is struck by the large and beautifully grown trees. But it is easy to forget that they are the final result of a prolonged interplay between a large number of trees with very different genetical endowments. It is only a very small part of the original number that has survived. Moreover, there is a tendency to make excuses for the less well-shaped, branchy, or in other ways poorer trees, and to regard them as having been less favoured by the environment. Try on such a site to see the younger generation; this gives a very different impression.

In the west of Vancouver Island, on the sheltered localities in Nootka Sound, there are the most magnificent stands of centuries-old Douglas fir. On a cleared area, which had lain for ten to fifteen years favourably exposed for sowing from the old stands, the author has, for example, observed distinct individual differences. There is positively no doubt that the whole of it is Douglas fir of a pronounced green and healthy coastal form; but by going through it more carefully one can also find occasional plants with such blue needles that they would be thought to belong to a geographical type occurring in the interior, if one had merely been confronted with them as single plants. There is also now and then a plant of another type, which might be found right up at Salmon Lake, and there are plants with coarse branches and curved stems without its being possible to see that they had been grown under more unfavourable external conditions than the finest slender, fast-growing young trees with the luxuriant green foliage.

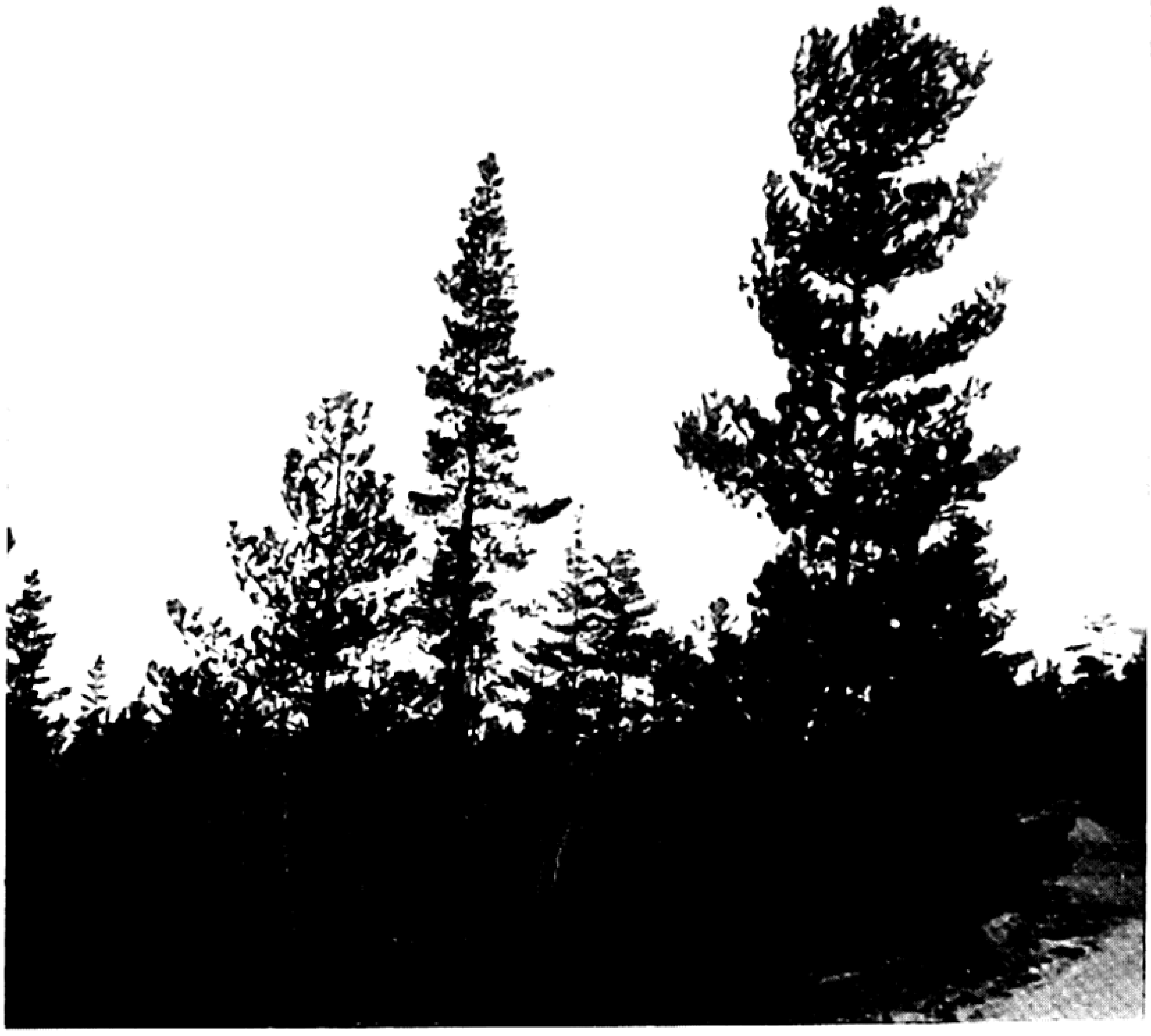


Fig. 67. *Pinus radiata* D.Don, Monterey pine. Young natural regeneration at Monterey. Note the individual variation in form. Photographed 15th March 1949.

In the struggle between the plants it may be the best fighters who win, and there must be a prolonged and hard " training " up to a time at which such large and fine trees are produced as are in the old stands. This takes a long time, and in our plantations we should want to reach a much quicker result, while we ought to avoid as far as possible the poorest forms, which may become specially undesirable.

In establishing planted stands (tree-farms) one usually wants to get as much as possible out of the seed. All the plants are utilized, nor is it possible to sort them out at so young an age. In the next place, all plants are put out at a regular spacing and under identical conditions. There is not the same waste of plants as in nature's self-sowings, and there is not the multiplicity of chance factors in the positions of the plants relative to one another. The opportunity to grow rapidly, which we give the plants by the regular distribution, helps the poor and the good plants to an equal extent. We thus become bound to intervene with thinnings in order to help the best plants. It is therefore a great economic advantage to be rid of the coarsest and most undesirable plants, so that as far as possible we plant only those plants which it will pay to harvest.

It is commendable that a considerable amount of planting of Douglas fir (tree-farms) has been taken up, in order to be able to gain experience of its technical treatment. It is important, however, that it should be accompanied by an at least equally energetic effort to raise plants from the best possible seed; and Douglas fir is indeed one of the most inviting subjects for improvement.

In contrast to Douglas fir, the Monterey pine (*Pinus radiata*) has its natural range over a very small region. It stretches only over some very small areas in Monterey County on the coast of California. On the other hand, it has become extremely widespread in cultivation, for which it is used in extensive plantations in New Zealand, in Chile, Australia, and South Africa. It is worth remarking that the trees of this species—distinctly " insignificant " from a geographical viewpoint—display an individual variation of structure which is at least as striking as that of Douglas fir.

When the natural range is so restricted, it is very natural to exclude right away any idea of types determined climatically. But that is only one aspect of the matter. Although Monterey pine in its occurrence so close to the Pacific Ocean is to a great extent affected by external conditions, it displays even there very considerable individual variation. This is best seen on the young, rather scattered regeneration which it has produced. One may put forward the hypothesis that this is due to " chance ", but the same impression of wide individual variation is got from Monterey pine in New Zealand; even in the older stands, which as a whole have had an almost luxurious development. Twenty-four years after the planting of one-year seedlings at about 2 × 2 m. ($6\frac{1}{2} \times 6\frac{1}{2}$ ft.) apart, trees have been measured with heights of well up to 40 m. (131 ft.) and of the finest form, while the rest have been of particularly variable growth and form right down to a considerable number of slow-growing, dead, or dying trees of the worst conceivable forms. It is difficult to explain such a variation without presuming a very definite genetical differentiation. The final evidence that it does behave in this way has been furnished by the New Zealand Forest Service by using graftings, and through the even older experiments with cuttings by the Forest Research Station at Canberra.

The New Zealand Forest Service has very kindly given permission to reproduce here the pictures in Figs. 68 and 69. It is to be hoped that they will contribute to serious thought wherever Monterey pine is taken up for economic utilization.

J. M. Fielding, in *Variations in Monterey Pine* (Forestry and Timber

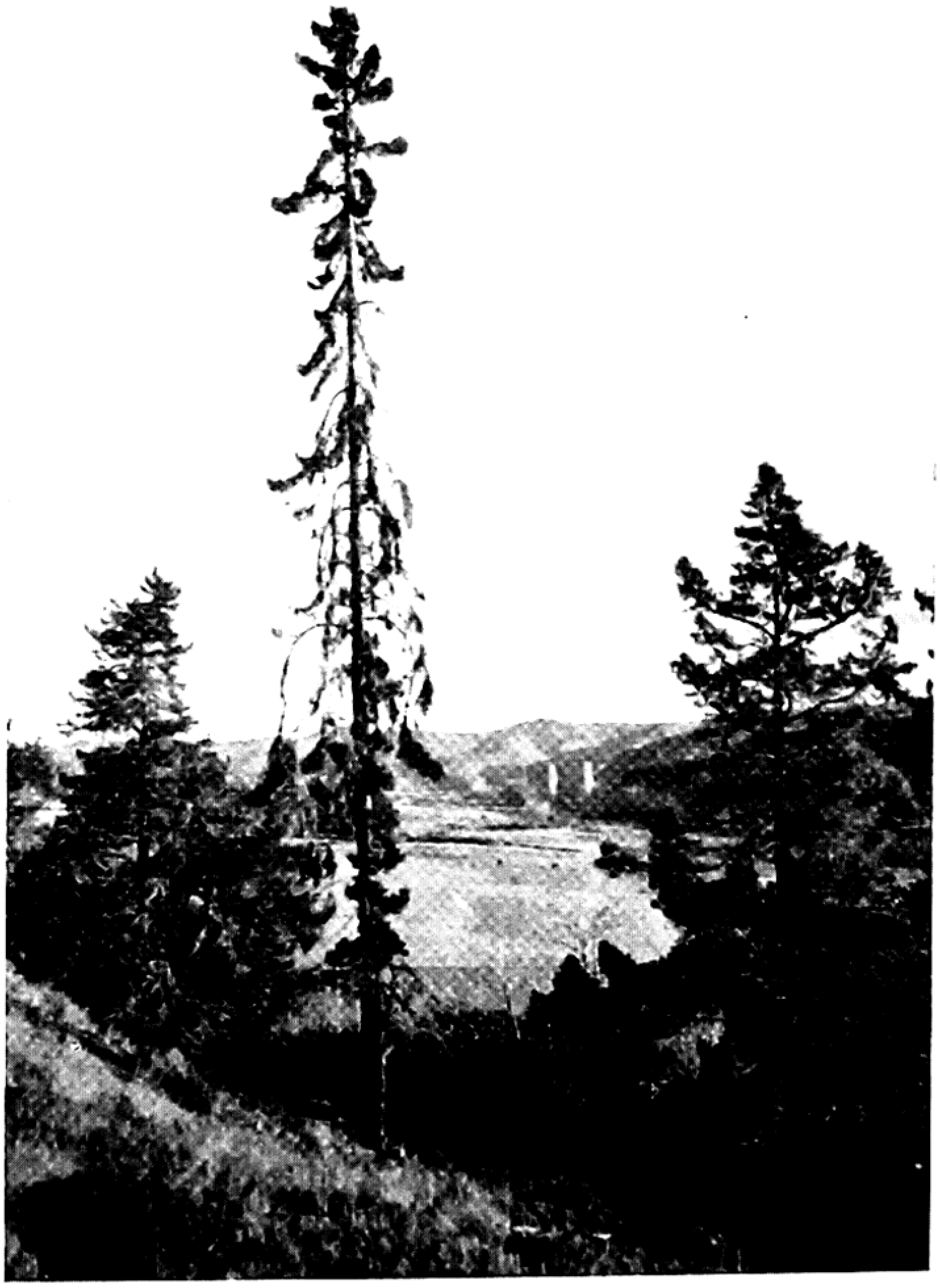


Fig. 68a. *Pinus radiata* D.Don, Monterey pine. Original tree, 88 valley, Nelson, about 65 years old. Height = 58 m. (190 ft.); D.b.h. = 114 cm. (36½ ins. Q.G.).

Bureau, Canberra. Bulletin No. 31, 1953) has made a brilliant contribution to its further use in cultivation. On the basis of experiments, for which M. R. Jacobs raised the first clones in 1938, an analysis thrilling for anyone engaged in forest-tree breeding was carried out.

For rate of growth it was found, at an age of twelve and a half years, that " one clone has produced almost five times as much wood per tree as the trees of another ". " Immunity from disease and insect attack . . . vary widely." " Indications were obtained that the inherent variation in the density of the wood of Monterey pine is large; spiral grain varies widely. . . .

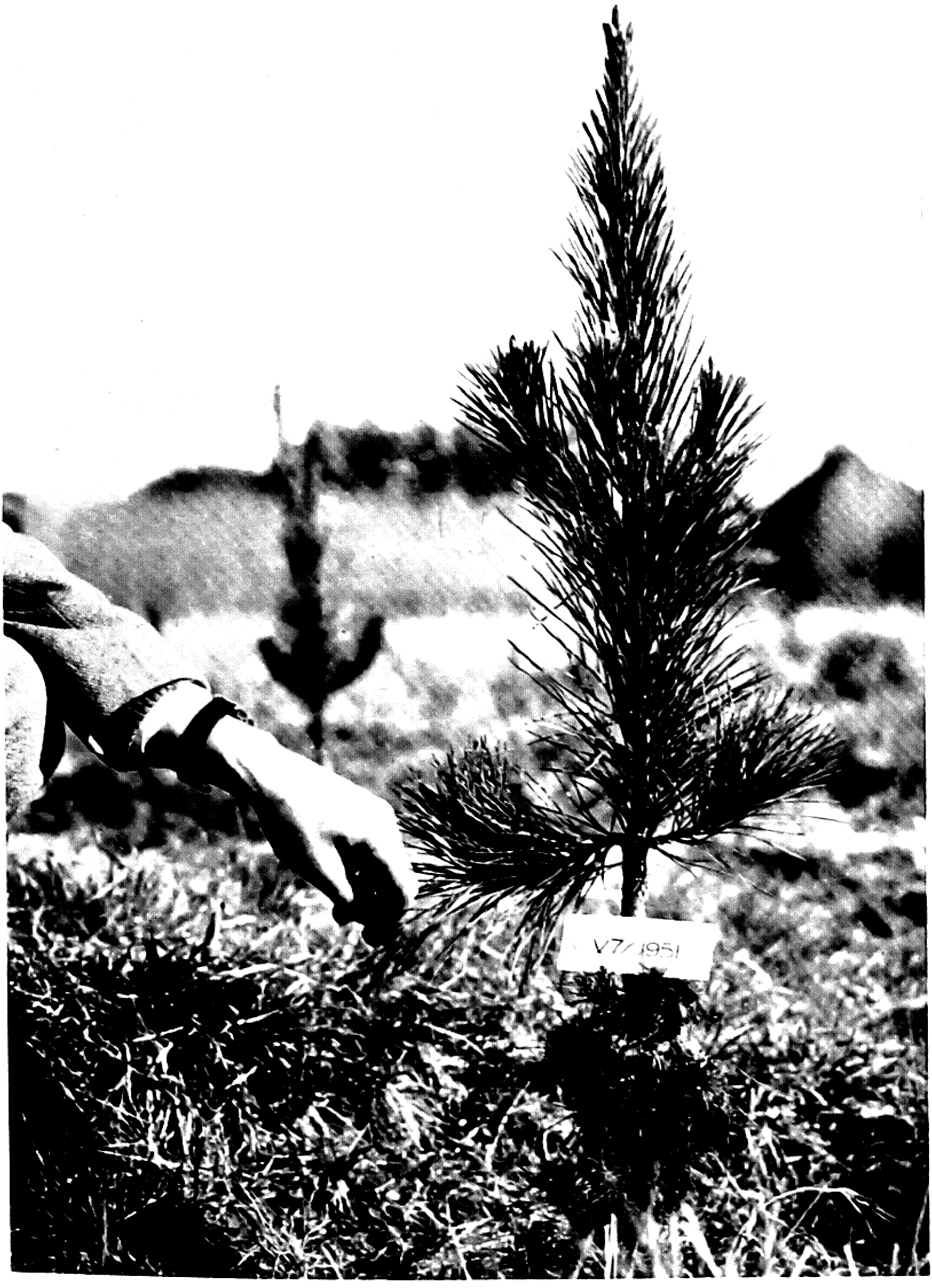


Fig. 68b. The tree in Fig. 68a grafted in 1951, photographed in August 1953. Figs. 68a and 68b New Zealand Forest Service photos.

Inherent variations are great in the tendency to produce defects such as bad knots and cone holes." Something similar was found in respect of the straightness, verticality and form of the trunk, crown characteristics, flowering, cones and seeds.

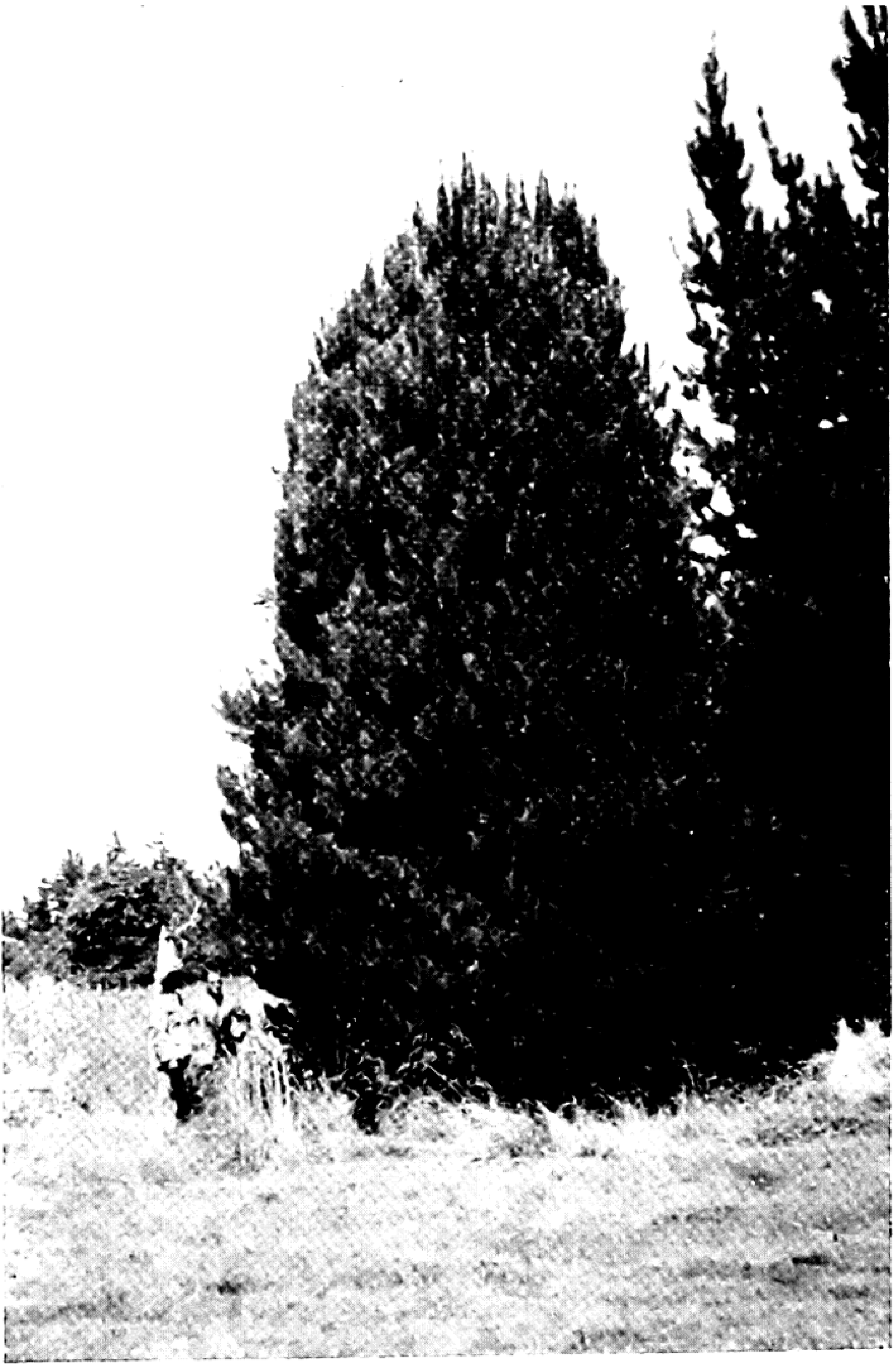


Fig. 69a. *Pinus radiata* D.Don, Monterey pine. Original tree, Napier, about 30 years old. Repeated forking.

FIELDING has been able to read all this from tree-shows, the material for which was collected in the Australian Capital Territory alone. It holds out high promise for extended improvement work.

In order to achieve the economically most favourable result, it must be the aim to the greatest possible extent to plant only what it can later pay to harvest. We must never forget that by planting forests there is serious interference with the order of nature. The loss of dead trees taking place naturally in the virgin forest may, in a planted forest of Monterey pine, for example, take a very different and more violent course, which may become the cause of destructive attacks by fungi and insects. As in densely populated, uni-

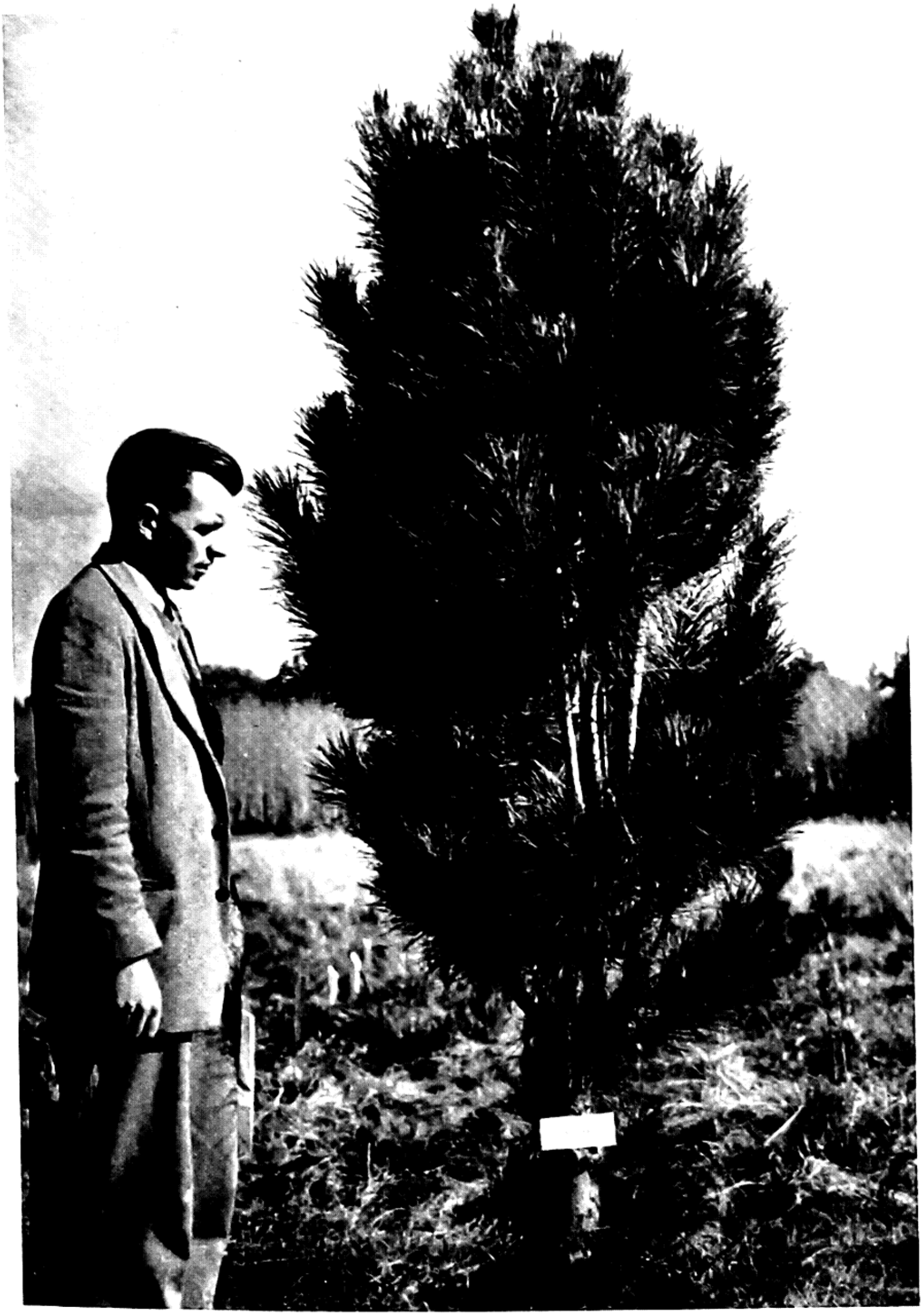


Fig. 69b. The tree in Fig. 69a grafted in 1950, photographed in August 1953. Figs. 69a and 69b New Zealand Forest Service photos.

form built-up areas, the sanitary service must be operative. To combine nature and cultivation may be risky. One must know exactly what one is about—and we know, amongst other things, that much money is employed in planting. We cannot therefore continue using nature's chancy population of a tree-species like Monterey pine. It must be improved, but that is a task to be undertaken with pleasure. It takes time, however, and it is therefore urgent.

In Monterey pine we have a conifer with great growth-energy and a wonderful capacity to take possession of new land. That has already been shown by its great popularity in afforestation under very varied external conditions. These outstanding qualities must not, however, cause us to overlook the fact that they could become a good deal better. It must not be forgotten that by far the overwhelming part of the Monterey pine grown in New Zealand and in other parts of the world has its origin in seed-collections in the hedges and small plantations established by the settlers. Seed was taken where it was easiest to collect the cones on the lowest, broadest, and most heavily fruit-bearing trees. The original selection from the natural stands in Monterey County was left to the settlers, who after the gold rush in California went off to new hunting-grounds in Australia. They can hardly be imagined to have paid great genetical attention to future production, when they acted according to the principle of collecting the cheapest seed possible.

There was a great demand for seed, when in New Zealand they were otherwise so far-seeing as to allow large gangs of the unemployed to plant forests in the depression years. By doing this New Zealand has obtained new valuable forests, but to-day we no longer have land almost gratis nor labour power at the low rate of wages prevailing under those conditions. The forest which now has to be created must be of a different and far better quality.

Poplars have been applied to quite a different kind of forest use. As was mentioned in the chapter on hybrids, the easy and formerly accidental occurrence of hybrids, combined with their almost universal propagation by cuttings, has led to almost the opposite extreme in the manner of their use. By the employment of cuttings for direct planting in the forest, both in Europe, North America, South America, New Zealand, and South Africa, magnificent, perfectly uniform stands have been obtained. They are undoubtedly valuable, but it cannot be concealed that they operate with relatively little volume of timber per unit of area and are perhaps unnecessarily uniform. With the narrowest conceivable selection from occasional trees in the form of cuttings from a single tree or very few trees there has been a rush to cultivate them. The reason why things have gone well on the whole may be explained by the fact that the vast majority raised have been hybrids.

If it is desired to grow the species, then the clones which exist in cultivation are all too few for a sound appraisement of their possibilities. As mentioned above, it is therefore valuable that in America, especially at the Harvard forest (Cabot Foundation), large-scale work on a more intensive study of the species has been taken up.

Provisional experience in cultivating poplar seems to confirm the experience gained, especially in agricultural plant-breeding, that a well-marked heterosis eliminates, as it were, the effect of a more or less good genotype. That is a great incentive to be on the look-out everywhere for the opportunity to make use of hybrid-vigour.

The poplars are only one example, due to their easy vegetative propagation from cuttings, and to the fact that nature has here given us an economically important tree-species with the sexes of the flowers separated into purely female and purely male trees. It was not necessary to resort to artificial measures of pollination in order to get the hybrids, which arrived, as it were, of their own accord, when trees of different sexes and species were planted together. This does not mean to say that other genera may not do the same thing as readily—and furnish something just as valuable—provided they are assisted on the way. That a poplar like *Populus canadensis* Moench., after its accidental occurrence as a cross between *P. balsamifera* L. and *P. nigra* L., had about two hundred years ago rapidly reached great popularity and is still much used, is simply due to the fact that it reproduces so easily from cuttings. Were this not so, it would certainly have rapidly sunk back into obscurity. All of it consists of cuttings from a single tree and from its cuttings, all of which are males.

Our equipment, our technical outfit, is now such that, combined with intensive studies of the biology of flowering, we are able to use for other tree-species, too, the heterosis often observed in the case of hybrids. We are certainly not bound to use only those hybrids which are inherently favoured by a capacity for easy vegetative propagation. By means of graftings and placing them judiciously in seed-gardens we can make sure of an abundant and constant production of seed for hybrids.

It is also worth while to consider *Eucalyptus*. Amongst these we have the world's tallest leaf-trees, and a number of the species are of great forestry value. Not only do they become large trees, but they also grow rapidly. It is an impressive sight to stand in the sample-plot of *E. regnans*, which is said to contain the tallest leaf-trees in the world and the tallest trees in the southern hemisphere. To a forester, however, it is even more gratifying that the age is put as low as about two hundred years (although occasional trees might perhaps reach an age of close on three hundred years), or to be introduced to natural regeneration at ten years of age with heights of nearly 30 m. (98½ ft.).

All the eucalypts important from the forestry viewpoint have their natural range in Australia alone. Only by man's help have they been taken long distances into almost every part of the globe and have thus proved to be perhaps the most outstanding cosmopolites. On previously treeless areas, with the use of eucalypts alone, purely artificial silviculture has been created, which on rotations of nine to ten years forms the basis of very considerable industrial concerns. Even more numerous, I suppose, are those places where these rapid-growing and in their own way quite inexacting trees are employed in forests, which have primarily to provide protection against erosion, furnish shelter from the wind, or contribute to dealing with surplus water.

Although in the planted forests of eucalypts there is commonly enough a name for the species, it is nevertheless difficult to deny that considerable uncertainty prevails with regard to the identification of the species. The frequent more or less satisfactorily substantiated statements about the occurrence of hybrids may also be mentioned. It is of the utmost importance that there should be undertaken increasingly more intensive work upon the systematy and biology of the species as a basis for breeding. The work which has been carried out in this field should by no means be underrated; it only requires to be stressed that it would be sound economy to take more energetic measures. This is certainly not a problem which concerns Australia alone; it affects everyone wishing to use eucalypts in whatever part of the world he may happen to be.

The material given to us by nature of Douglas fir, Monterey pine, poplar, *Eucalyptus*, and many other groups of trees not mentioned here like spruce, teak (Fig. 70), *Agathis*, etc., is in the most inviting way tempting for intensive utilization. We have up-to-date equipment for clearing the forest, transport of timber, and for its further manufacture; nor must it be forgotten that planting machines exist. Moreover, there is easy access to useful material for the study of the taxonomy, biology of flowering, and many other features of trees. This should not merely be studied as a " botanical science ", but expanded to a technical aid in building up silviculture.

The botanist should not be allowed to wander with his vasculum only. Give him a jeep, extension ladder, and assistance to study the flowering in the tall " inaccessible " tree-crowns, so that he does not have to restrict himself to the herbs in the forest. Let the forester also be with him, so that together they can select the finest trees and stands. They have first of all to be preserved and studied on the site; but the material (the valuable genes) must also be incorporated in the work of the research stations by controlled pollinations and graftings in tree-shows, etc. Motor and air transport is the modern solution of the problem of rapid despatch of the vegetative material. Scions of Douglas fir have been grafted in Denmark four days after their despatch from California, and pollen has arrived just as quickly from the opposite direction.

It is important to arrange to build up the more expensive equipment with regulated temperature and moisture for preserving the seed, but we must not forget to use the cheap grafting-knife in establishing the "seed-gardens" of the future.

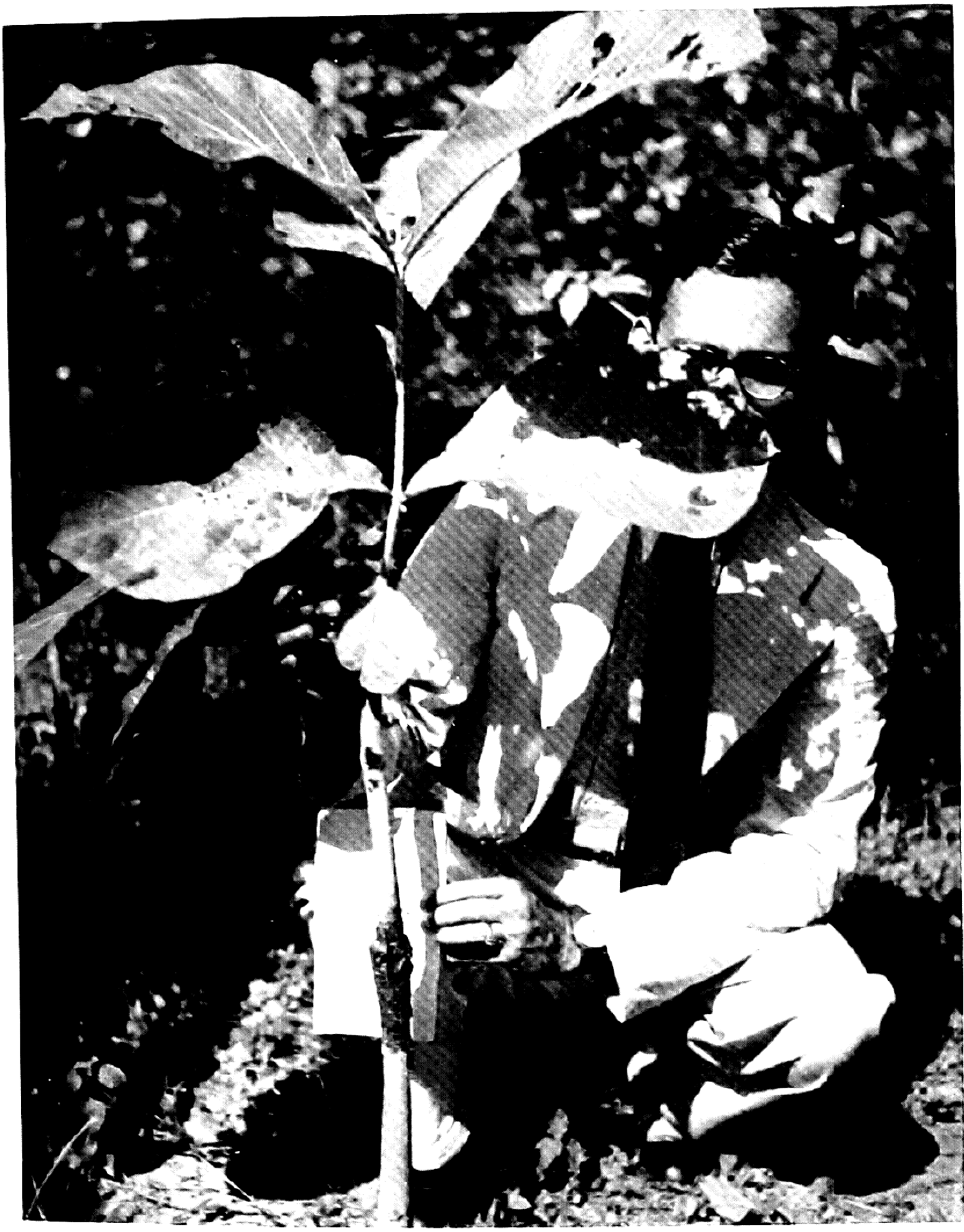


Fig. 70. Teak (*Tectona grandis*). Graft with root-stock about 5 or 6 years old and scion from a large tree, made in 1951. Photographed in 1953. *Photo,* H. S. Rao, Forest Research Institute, Dehra Dun, India.

As soon as we find ourselves with good seed, planting and planting-machines will certainly come into greater use. In step with improved quality of the seed a further expansion of equipment for forest planting will take place. The technical progress, which causes nature's growing-stock to disappear at a steadily increasing rate, will gradually be converted for use in building up the forest. This is hindered only by the inadequate effort of forestry to produce seed from trees of better quality.

Bull-dozers break the way for the felling of forests, but roads are also necessary when they have to be planted. What a waste of capital it is to make roads only for the transport of the mature trees! These roads should also be used for planting and tending the new forest. The aim must be a perpetual " manufacturing " of forests which furnish a sustained yield.

So long as the felling goes on with its present intensity, it is possible that it may be good business to plant forests with the plant material already available. Every benefit realized by breeding will contribute, however, to greater and cheaper production and hence to greater profit.

Let us therefore use our equipment, our tools, from the simple grafting-knife to the expensive research stations, in order to work with controlled pollination, vegetative propagation, seed-gardens, tree-shows, cytology, and much more in order that the plant-breeders in forestry may make their contribution to the development of silviculture in the service of the community.

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